When and where to lay your eggs?

How decision problems arise and are solved by phytophagous insects

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In the light of the moon, a little egg lay on a leaf.
Eric Carle, The very hungry caterpillar

Abstract

A substantial portion of the millions of insect species on earth are phytophagous, and the great majority of these species is oviparous—they reproduce through larvae or nymphs that hatch from eggs laid by female insects on specific host plant species. When a female insect lays their eggs, however, she is repeatedly faced with the decision problem of ovipositing on lower-quality host plants or waiting out for higher-quality ones. Since her offspring develop differentially well depending on which host plant species they are raised upon, a mother's oviposition decisions carry significant fitness costs and benefits. At the same time, females are pressed for time and for eggs in every oviposition decision they make—if they are too picky, they may run out of lifetime before all eggs have been laid and thus become "time-limited"; if they are not choosy enough, they may run out of eggs before their lives are over and thus become "egg-limited".

This thesis employs diverse theoretical approaches to examine how decision problems arise during the oviposition of phytophagous insects and how they are solved by female insects in their oviposition strategies. I begin by using analytical optimization models to show how the well-known life-history trade-off between survival and reproduction may lead to widely varying evolutionarily stable levels of egg and time limitation, the quantitative details of which depend on the trade-off's shape and parameters. These findings also demonstrate that, while the risks of both egg and time limitation need to be evaluated on a case-by-case basis, neither phenomenon can be safely ignored in evolutionary studies of strategic insect oviposition. I then employ more schematic models to examine whether partitioning the fitness costs and benefits of each oviposition decision into opportunity costs mediated by time and by eggs is a useful practice to analyze oviposition strategies. I find that, in general, schematic time and egg costs will have to be conceptualized with great care to deliver insightful results, and that detailed evolutionary models may therefore represent more fruitful tools to study strategic insect oviposition.

After studying the basis of the insects' oviposition decision problems, namely how egg and time limitation may come about, I examine how generalist oviposition strategies can evolve from more specialist ones. Since most insects are specialists, but since generalism is a necessary intermediate step in the many host switches that have occurred over evolutionary time, the evolution of generalism is of key interest in the oviposition of phytophagous insects. My results confirm that unreliability of host plant availability may lead females to become more generalist and include novel hosts in their diet breadths on which larvae develop less successfully than on ancestral hosts. Using a combination of optimization and population genetic models as well as individual-based simulations, I show that generalism only evolves under restrictive conditions if host availability varies *spatially* but more readily when it varies *temporally*. This is because spatial variation in host availability can lead to emergent source-sink dynamics which favor specialist oviposition strategies adapted to highly productive habitats with more-than-average high-quality hosts. Conversely, temporal variation in host availability favors generalist strategies that fare well also in times with lower-than-average high-quality hosts. I explore the latter scenario using a simulation study of the orange tip butterfly (*Anthocharis cardamines*), a species whose larvae are phenologically specialized on flowers and seeds but whose females are oviposition generalists. My results suggest that this oviposition generalism may indeed result from the larvae's phenological specialism which reduces host availability because it shortens the time windows during which individual host plants are suitable for successful larval development.

Taken together, the approaches presented in this thesis showcase the usefulness of different theoretical methods to examine strategic oviposition in phytophagous insects. The resulting findings have consequences for empirical studies of insect oviposition, for instance with regard to which factors insects include in their oviposition decisions or how insects respond to geographically varying host plant abundances. Moreover, I discuss

in detail the potential for future theoretical studies to examine other, potentially more cognitivist questions of strategic insect oviposition. In summary, while general findings on strategic oviposition valid across *all* phytophagous insect species can hardly be generated, theoretical studies represent a productive approach towards a deeper understanding of the oviposition strategies of *specific* insect species where, ideally, much is known about both their ecology and their development.

Zusammenfassung

Von den Millionen Insektenarten der Erde ist ein großer Teil phytophag. Wiederum die große Mehrheit dieser Arten ist ovipar—sie vermehren sich durch Larven oder Nymphen, die aus von ihren Müttern auf bestimmte Wirtspflanzen gelegten Eiern schlüpfen. Bei ihrer Eiablage stehen phytophage Insektenweibchen wiederholt vor der Entscheidung, ihre Eier entweder auf Wirtspflanzen geringerer Qualität zu legen oder aber auf höherwertige Wirtspflanzen zu warten. Da die Wahl der jeweiligen Wirtspflanze einen großen Einfluss auf die Entwicklung der Larven hat, tragen die Eiablage-Entscheidungen der Mütter erhebliche Fitness-Konsequenzen. Gleichzeitig stehen Insektenweibchen bei der Eiablage nicht nur unter Zeitdruck, sondern auch unter "Eidruck"—wenn sie allzu wählerisch sind, könnten sie bei ihrem Tod nicht alle Eier gelegt haben und wären damit "Zeit-limitiert"; wenn sie aber nicht wählerisch genug sind, könnten sie bereits vor ihrem Tod alle Eier gelegt haben und wären damit "Ei-limitiert".

Diese Doktorarbeit nutzt unterschiedliche theoretische Ansätze um zu prüfen, wie Entscheidungsprobleme bei der Eiablage phytophager Insekten entstehen und wie Insekten diese Probleme in ihren Eiablagestragien lösen. Zunächst benutze ich analytische Optimierungsmodelle um zu zeigen, wie die bekannte Austauschbeziehung zwischen Überleben und Fortpflanzung zu einer großen Bandbreite an evolutionär stabilen Wahrscheinlichkeiten von Zeit- und Ei-Limitierung führen kann. Dabei hängen die quantitativen Details dieser Wahrscheinlichkeiten von der Form der Austauschbeziehung und ihrer Parameter ab. Diese Ergebnisse zeigen auch, dass zwar die Wahrscheinlichkeiten von Ei- und Zeit-Limitierung in jedem Fall einzeln untersucht werden müssen, dass aber keines dieser beiden Phänomene in der evolutionären Analyse von Eiablage-Strategien vernachlässigt werden sollte. Anschließend benutze ich schematischere Modelle um zu prüfen, ob es eine nützliche Praxis für die Analyse von Eiablage-Strategien ist, die Fitness-Kosten und -Nutzen jeder Eiablage-Entscheidung in solche Opportunitätskosten aufzuteilen, die durch Zeit vermittelt werden, und solche, die durch Eier vermittelt werden. Dabei ergibt sich, dass derartige schematische Ansätze zu Zeit- und Ei-Kosten mit großer Sorgfalt konzipiert werden müssen, damit sie aufschlussreiche Ergebnisse liefern. Deshalb könnten ausführliche evolutionäre Modelle produktivere Werkzeuge für die Untersuchung von Eiablage-Stragien darstellen.

Nachdem ich die Grundlage der Entscheidungsprobleme von Insekten bei ihrer Eiablage untersucht habe—nämlich wie Ei- und Zeit-Limitierung entstehen können—behandle ich nun, wie aus Spezialisten, die ihre Eier auf eine oder wenige Wirtspflanzen legen, Generalisten evolvieren können, die mehr Wirstpflanzen nutzen. In der Eiablage phytophager Insekten ist die Evolution von Generalismus eine zentrale Frage, weil einerseits die meisten Insekten Spezialisten sind, andererseits aber Generalismus einen notwendigen Zwischenschritt darstellt in den vielen, phylogenetisch dokumentierbaren Wirtspflanzen-Wechseln in der evolutionären Vergangenheit. Meine Ergebnisse bestätigen, dass Unzuverlässigkeit in der Verfügbarkeit von Wirtspflanzen Insektenweibchen dazu bringen kann, generalistischere Eiablage-Strategien zu entwickeln und auch solche Wirtspflanzen in ihr Wirts-Spektrum aufzunehmen, auf denen ihre Larven sich weniger erfolgreich entwickeln können als auf den anzestralen Wirtsarten. Mit einer Kombination von Optimierungs- und populationsgenetischen Modellen sowie Individuen-basierten Simulationen zeige ich, dass Generalismus nur unter relativ eingeschränkten Bedingungen evolviert, wenn die Wirtspflanzen-Verfügbarkeit *räumlich* variert, aber leichter entstehen kann, wenn diese Verfügbarkeit *zeitlich* variiert. Dieser Befund liegt darin begründet, das räumliche Variation der Wirtspflanzen-Verfügbarkeit zu emergenten Quellen-Senken-Dynamiken führen kann, durch die Eiablage-Strategien von Spezialisten einen Vorteil haben, die an überdurchschnittlich produktive Lebensräume mit einer überdurchschnittlichen Anzahl hochwertiger Wirtspflanzen angepasst sind. Umgekehrt begünstigt

die zeitliche Variation der Wirtspflanzen-Verfügbarkeit Eiablage-Strategien von Generalisten, die auch in Zeiten mit unterdurchschnittlicher Anzahl hochwertiger Wirtspflanzen gut abschneiden. Letztere Situation untersuche ich mit Hilfe einer Individuen-basierten Simulation, die auf den Aurorafalter (*Anthocharis cardamines*) zugeschnitten ist. Dieser Schmetterling ist besonders interessant, weil seine Larven hinsichtlich der Phänologie ihrer Wirtspflanzen auf deren Blüten und vor allem Samen spezialisiert sind, während die Weibchen in ihrer Eiablage Generalisten sind und ihre Eier auf unterschiedliche, kreuzblütrige Wirtsarten legen. Meine Ergebnisse deuten darauf hin, dass dieser Eiablage-Generalismus in der Tat ein Resultat des phänologischen Spezialismus der Larven sein kann, da dieser Spezialismus die Wirtspflanzen-Verfügbarkeit reduziert, weil er die Zeitfenster verkleinert, in denen bestimmte Wirtspflanzen für eine erfolgreiche Entwicklung der Larven geeignet sind.

Zusammen genommen zeigen die in dieser Arbeit präsentierten Ansätze die Nützlichkeit verschiedener theoretischer Methoden zur evolutionären Untersuchung der strategischen Eiablage bei phytophagen Insekten. Die daraus resultierenden Ergebnisse haben Konsequenzen für die empirische Forschung an der Eiablage von Insekten, zum Beispiel in Bezug auf die Frage, welche Faktoren Insekten in ihren Eiablage-Entscheidungen berücksichtigen oder darauf, wie Insekten auf unterschiedliche Wirtspflanzen-Häufigkeiten in unterschiedlichen Lebensräumen reagieren. Weiterhin diskutiere ich im Detail die Möglichkeit, mit zukünftigen Studien andere, möglicherweise kognitivistischere Fragen der strategischen Eiablage phytophager Insekten zu untersuchen. Insgesamt lässt sich also sagen, dass zwar durch theoretische Studien, wie sie in dieser Arbeit präsentiert werden, kaum Erkenntnisse über Eiablage-Stragien gewonnen werden können, die für *alle* pflanzenfressenden Insektenarten gelten, dass aber theoretische Methoden produktive Ansätze darstellen, um zu einem tieferen Verständnis des strategischen Eiablage-Verhaltens *bestimmter* Insektenarten zu gelangen, bei denen im Idealfall viel über ihre Ökologie und ihre Entwicklung bekannt ist.

Inhaltsverzeichnis

1 Introduction: The challenges of strategic oviposition

1.1 Phytophagous insects and their reproduction

Insects make up a major portion of the global biodiversity of eukaryotes: While recent studies estimate that between 5 ± 3 and 11 million species exist in total [14, 80], the number of insect species alone has conservatively been estimated at around 5 million [35].[1]. Deriving a robust estimate for the proportion of phytophagous insects among these species is difficult at best, but their magnitude is likely to be significant. A study on tropical beetles, for instance, found more than 60% of the examined 1100 species to be herbivores (summarized in [74]), and a meta-analysis on insect herbivore diversity patterns suggests that herbivore proportions likely are not disproportionately lower in the temperate zones [82]. Moreover, phytophagous insects are not only rich in species number but also in the ecological roles they fulfill, be it as pollinators, crop pests, food for predators and parasitoids, or as hosts for reproductive parasites like *Wolbachia*.

With their large diversity and, in part, good accessibility in field and laboratory, insects have become model systems for the exploration of reproductive behavior. Since the large majority of insects are oviparous—they reproduce by laying eggs that hatch into nymphs or larvae—oviposition is central to the evolution of plant-insect and, more generally, host-parasite interactions.

In phytophagous insects, eggs are laid on or in the vicinity of certain host plants upon which the resulting larvae then feed and develop. Evidence indicates that these insects actively choose oviposition sites: In choice assays where insects are offered two different host plants, an individual female will often lay many eggs on one host but few or none on the other (e.g. [104]). To make these choices in their natural environments, female insects have evolved various host plant assessment behaviors (see below). Additionally, a number of studies have demonstrated that insect oviposition preferences for different host plants are heritable, genetically encoded traits (summarized in [106]). As a result, understanding the evolution of oviposition preferences and oviposition site choice is critical to our knowledge of the evolution of host choice [17].

Many examples exist in the literature demonstrating that female insects assess the quality of encountered host plants for oviposition. In the orange tip butterfly, *Anthocharis cardamines*, for instance, deterrent pheromones exist that let females identify leaves where an egg has been laid previously [19]—a behavior that is potentially of large benefit because larvae have been described to be cannibalistic [20]. In the same species, females have been

[1] A large range of variation exists for these values, especially their upper bounds. Estimates for the total number of eukaryote species range from 2 to 100 million [14]; species numbers of up to 30 million have been suggested for insects alone (summarized in [35]) The fact that, as of 2013, only 1.5 million of these species have been formally described demonstrates the degree of uncertainty associated with all these estimates [14].

observed to reject host plants for oviposition if the plant stem bends under the female's weight [127]—likely an indication of insufficient resources for successful larval development on this plant. Additionally, female orange tip butterflies even distinguish between plants with different ploidy levels of the same host species [3]. Finally, female small white butterflies, *Pieris rapae*, actively evaluate potential host plants by drumming on leaf surfaces with their fore-tarsi so that gustatory receptors can acquire information on the chemical composition of a given host plant [47].

Equally interesting are the many examples that demonstrate how specialized insects are in the detoxification of foods they take up from their plant hosts. These cases exemplify the long history of co-evolution between phytophagous insects and their host plant species [26]. The brassicaceous plants that are host to such butterfly species as the small white, for instance, contain large amount of glucosinolates—components related to the mustard oils that make these plants attractive for human use. The butterfly larvae, however, have co-evolved with their plant hosts to possess an aromatic nitrile metabolism that can metabolize these glucosinolates to, in the end, aldehyde and cyanide [107]. Cyanide itself is a potent toxin affecting cell respiration, but pierid larvae apparently are highly tolerant to cyanides and may even be able to channel these toxins to amino acid production [107]. Particularly insightful with regard to the question of what came first, oviposition preferences or detoxification capabilities, is the fact that the pierid butterflies' cyanide-pathways are thought to be an ancestral feature of their metabolism, prior to their feeding preferences for glucosinolate-containing brassicaceaes [107].

1.2 Oviposition decisions of phytophagous insects

Oviposition decisions in insects are a prominent example of behaviors that have a direct effect on fitness. Larvae may grow better on one host species but worse on another; predation pressure may differ between host species; or adult feeding preferences may be different from their oviposition preferences (e.g. [39, 110, 124]). In the case of differential larval growth and survival—likely the most prominent consequence of oviposition decisions for reproductive success—these fitness effects are mediated by the positive correlation between adult body size and nutritional quality during development that is visible in many insects [24]. Host choice is also a crucial decision on the population level because host shifts may lead to reproductive isolation and incipient speciation [24, 30]. Such host shifts can proceed at impressive speeds—the apple race of the apple maggot (*Rhagoletis pomonella*), for example, has significantly reduced its response to volatile fruit odors of hawthorn and increased its preference for apple in the past 150 years [70].

During oviposition, however, phytophagous insects face several particular challenges. The best hosts for offspring development may be rare, but using suboptimal hosts for oviposition is costly because of decreased larval performance. Insects thus need to strike a balance between laying eggs only on optimal hosts and also accepting less favorable ones. From an evolutionary standpoint, insects are expected to evolve oviposition strategies that are optimal in the sense that they produce highest fitness returns—or, as a proxy, in terms of lifetime reproductive success—in the insects' typical environment.

1.2.1 Time and egg limitation

As in all iteroparous organisms, reproduction in insects is constrained by a fundamental trade-off between current and future reproduction [4]. The time used to find a host and lay an egg now cannot be used for oviposition in the future, and an egg laid now obviously cannot be laid in the future. Every oviposition thus carries opportunity costs mediated by time and mediated by eggs [94].

At the same time, the number of eggs that a female lays will always be limited either by her lifetime, so-called *time limitation*, or by the number of eggs she carries, so-called *egg limitation*. Simply put, if a female dies before laying all her eggs, her reproduction was limited by the time available and she is called "time limited"; if she dies after laying all her eggs, her reproduction was limited by the number of eggs available and she is called "egg limited" (see figure 1.1).

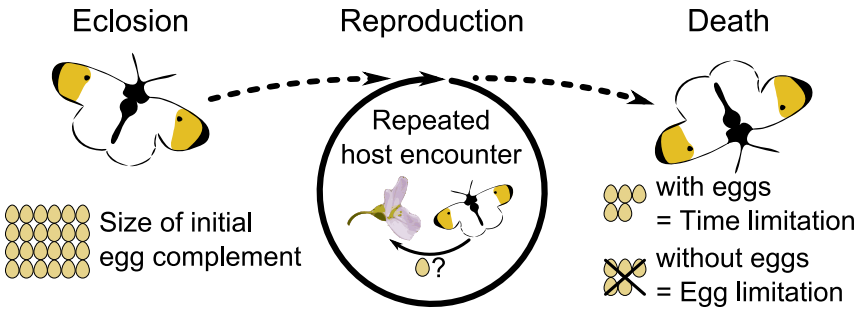


Figure 1.1. Egg and time limitation in the context of a simplified insect life history. An adult insect ecloses from its pupa with a certain number of eggs, reproduces by repeatedly encountering host plants and potentially accepting these for oviposition, and dies. If the insect still possesses eggs at its death, it has become time limited; if not, it has become egg limited. Cuckoo flower and orange tip based on pictures by P. Appleton and B. Busschots (CC-BY).

In turn, time and egg limitation determine the costs and benefits of different oviposition strategies. For instance, pure time limitation favors generalist oviposition on all available hosts because individuals will always have more eggs than they can lay. Pure egg limitation, on the other hand, favors specialism on only the optimal host, no matter how rare, because individuals will never be limited in the time available for host search and oviposition. In real world situations, however, both egg and time limitation occur with non-zero probabilities. Individual insects thus have to find the optimal mixture of specialism and generalism for their oviposition strategies. Finding the optimal oviposition strategy is an interactive process because, as is intuitively clear, oviposition decisions alter the probabilities of becoming egg or time limited, thereby influencing a strategy's fitness costs and benefits (see figure 1.2).

As a result, estimating the influence of time and egg costs in real-life ovipositing insects may help shed light on the factors that shape optimal oviposition strategies [93, 103]. However, past research on insect oviposition often considered either only egg or only time costs, thus assuming individuals to be either always egg- or always time-limited [15, 68, 97]. Since insects neither are immortal nor carry an infinite number of eggs, such presuppositions likely lead to misinterpreting real-life oviposition strategies.

Previous empirical studies of oviposition and host choice in phytophagous insects some-

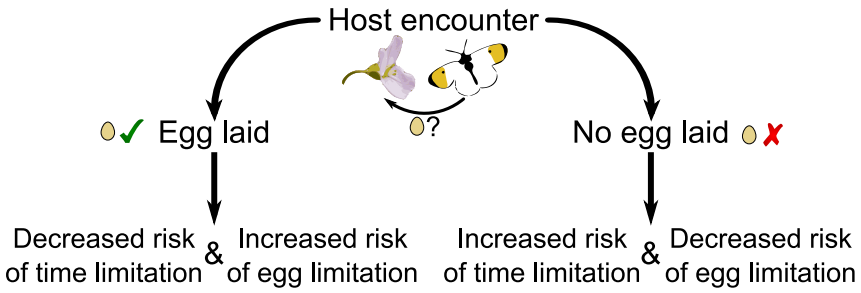


Figure 1.2. The consequences of oviposition decisions. Each oviposition decision affects the probabilities of time and egg limitation. Accepting a host plant upon encounter and laying an egg decreases the risk of time and increases that of egg limitation; rejecting a host and not laying an egg does just the opposite. Image credits as in fig.1.1.

times produced puzzling results. While one might expect females to prefer hosts where larvae perform best, such *preference-performance correlations* are often absent in nature [110] and may be the exception rather than the rule [39]. Female butterflies may oviposit on bad hosts but reject good hosts [52], choose hosts that are lethal to larvae (summarized in [51]), or even drop their eggs in mid-air [21]. Various explanations have been brought forward for these phenomena, either involving additional influences to larval fitness, environmental stochasticity, or host distribution patterns (reviewed in [113]). Egg and time limitation are likely important factors in the questions of preference-performance correlations because they influence the fitness costs and benefits of, for instance, laying eggs on suboptimal hosts.

1.3 Determination of host preferences

Researchers have previously used the term host preference to indicate both the rank order with which insects accept different hosts for oviposition and the quantitative degree by which insects prefer one host over another (summarized in [105]). In the context of this thesis, I take an empirical definition of the term "preference" where preferences are measured as the proportion of eggs found a given host species in relation to the relative frequency of that host species (see figure 1.3). In this context, a value larger than one indicates a differential preference for that host, and values for different host species can be compared and used to determine an insect's preference ranks as well as their relative degrees. Empirical studies have used similar approaches and analyzed host plant utilization by comparing the residuals from regressing the number of eggs on each plant species in relation to the number of sites where these plants were found [127].

Preference hierarchies are a very general algorithm for decision making in organisms [16]. Due to their common architecture, preference hierarchies can produce behavioral outcomes ranging from extreme specialism to broad generalism. They can therefore mediate between the two most extreme options of the specialism-generalism-dichotomy since changes in preference hierarchies over evolutionary time may lead to shifts from generalism to specialism as well as to host range shifts within specialism or generalism ([54, 125]). This is due to the fact that preference hierarchies determine individual niche breadth, and changes in prefer-

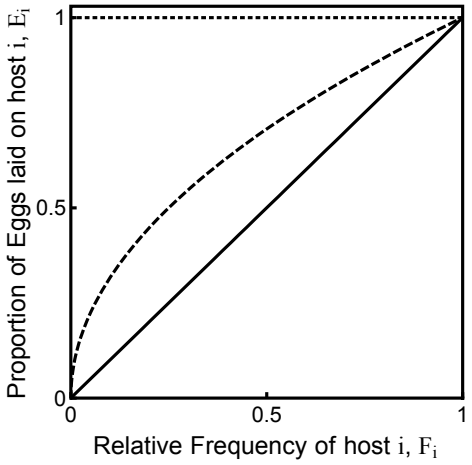


Figure 1.3. Realized oviposition preferences can be described as the proportion of eggs laid on a given host in relation to that host's relative frequency. In true generalist oviposition strategies, egg distributions are identical to host plant frequencies (solid line) whereas specialist strategies show distributions of eggs deviating from those of host plants (dashed line, type II functional response; dotted line, complete specialization on single host species irrespective of its frequency).

ence hierarchies can thus alter both niche breadth and niche position in "host plant space". As a result, preference hierarchies may play a leading role in the foraging ecologies and life history strategies that constitute a population's (or species') niche breadth and behavioral variation (e.g. [111]). Especially within the context of host shifts, changes in preference hierarchies may also be important factors for host race formation [123] and, possibly, ecological speciation [23].

Throughout this thesis, individual preference hierarchies are assumed to be genetically determined and uninfluenced by environmental cues such as abundance of potential hosts. There is a wealth of evidence in support of the first claim, indicating that oviposition preferences are heritable and that genetic variation in oviposition preferences exists both within and between butterfly populations (summarized in [105]). The latter claim, however, receives more ambiguous support with some papers finding evidence for adaptive learning of host encounter rates in ovipositing insects and others failing to do so (summarized in [85]). As a result, assuming the absence of environmental influences on the insects' genetically determined oviposition preferences represents a simplifying, but not necessarily always justified, assumption for the sake of developing clear and tractable mathematical models.

A general complication that arises from the genetic determination of host preference is the potential mismatch between host availability and oviposition preferences. For instance, individuals which prefer locally uncommon hosts face a potential disadvantage since they may be unable to find suitable oviposition sites within their local habitat. However, since every adult must have successfully developed on some host plant, individuals are likely to have been raised on a plant that is a highly-ranked host and/or a species where larvae perform well. Thus, preferred host plants are more likely to be absent form the immediate surroundings if either host abundance changes quickly over time or if post-hatching dispersal occurs and

the particular host plant is uncommon in neighboring habitat patches. As a result, patterns of environmental variation, specifically temporal and spatial autocorrelation, are key factors in determining the accuracy of genetically determined oviposition preferences with regard to host availability (see section 1.4 and [75]).

Overall, genetically determined preference hierarchies reemphasize an essential feature of habitat quality: The optimal habitat for a species or a population does not exist. Instead, each individual perceives its surroundings differently and assesses the quality of these surroundings according to its own phenotype and, potentially, its overall status or condition. Experimental studies on birds in support of this general view showed food provisioning to result in earlier laying dates and increased clutch sizes when compared to unprovisioned control groups (as reviewed by [76]). Thus, individuals seem to assess the quality of their specific habitat (in this case represented by that habitat's resource content) and adjust their behavior accordingly instead of adhering to a hypothetical laying date or clutch size that is optimal on a species or population level. Naturally, individuals can also take into account other factors than their nutritional status (e.g. [42, 61]).

1.3.1 Modeling strategic insect oviposition

The evolution of strategic insect oviposition has attracted a magnitude of modeling efforts in the past. To my knowledge, the first mention of 'oviposition tactics' in a modeling context is made in Mitchell's work on individual decision rules in the bean weevil (*Callosobruchus maculatus*), where he uses 'tactics' synonymously with 'strategy', the latter more frequently than the former [79]. The next mention of either concept, however, does not occur until almost a decade later by Yoh Iwasa and colleagues [50]. In this important paper, the authors deliver a comprehensive theoretical study of strategic oviposition in parasitoid insects by applying insights from optimal foraging theory to the question of how life span and egg number shape egg-laying strategies. Most importantly, the authors challenge the previously common assumption that time is the main limiting factor and that rate-maximization therefore is the strategy favored by evolution (e.g. [68]). More details on the consequences of this assumption and its validity are presented and discussed in chapters 2 and 3 of this thesis.

With specific regard to phytophagous insects, optimal oviposition behavior had already been studied a few years prior when John Jaenike modeled the question of whether insects should accept or reject a given host plant upon encounter, although this study focused on the timing *during* host searches when particular host species should be accepted for oviposition [51]. In short, Jaenike found that insects should become less picky in their host choices with increasing unsuccessful search time. This finding was later corroborated by theoretical studies using dynamic programming to show that, indeed, insects are expected to change their acceptance rates dynamically to become less choosy over the course of their lifetimes in response to how many eggs they still carry (see [71], as well as [78] for a review of empirical data).

In the context of this thesis, I favor a combination of tractable analytical models of insect oviposition (chapters 2–4) with more complex individual-based simulations (chapter 5) over the technique of dynamic programming. This is because each of these methods, analytical modeling and simulation, has specific advantages that make them particularly useful in combination. On the one hand, I believe that analytical modeling results are more easily interpretable in their quantitative details and in the ways they relate to oviposition strategies than the decision rules produced by the backward inductive logic of dynamic programming. On the other hand, the forward logic of individual-based simulations offers an intuitive

grasp of how variation in insect oviposition behavior affects reproductive success, with the added benefit of the potential complexity offered by individual-based simulations due to their modular nature. As a result, insights from analytical models can be productively combined with simulation results to yield a more complex, though far from complete picture of strategic insect oviposition.

Past analytical work on strategic insect oviposition necessarily tended to focus on specific questions within this wide field. A number of studies, for instance, concentrated on the question whether eggs or time are more important in determining insect oviposition strategies (see [93, 103])—a discussion that goes back to the previously-mentioned article by Iwasa and colleagues published more than decade earlier [50]. Though seemingly of minor importance, the question of time and eggs has major effects on oviposition behaviors because, if only time is of importance, insect should behave as rate-maximizers in their oviposition strategies whereas, if only eggs matter, they should behave as quality-maximizers. The relative importance of time and eggs for strategic oviposition, however, depends critically on assumptions regarding the underlying trade-offs between survival and reproduction that lead to insects running out of eggs in the first place, as is shown in detail in chapter 2. As a result, assuming that only eggs or only time are important can have large effects on insect fitness estimations.

Regarding simulation models, a large amount of prior work exists on questions of insect optimal oviposition. For instance, already Mitchell used computer simulations to check his model on bean weevil oviposition decision rules against empirical data [79]. In a similarly early example, Jones used computer simulation to examine the oviposition movement patterns of small white butterflies, *Pieris rapae* [58]. Recent, more complex models on strategic oviposition behavior seem to be rare, however. For example, Olofsson and colleagues employed an individual-based model to examine different bet-hedging strategies regarding the evolutionary trade-off between egg size and number [83]. This approach is very general in nature—not even specified to plants or animals—and aims to show the broad possibility of phenotypic polymorphisms arising as a consequence of evolutionarily stable mixed bet-hedging strategies [83]. By contrast, simulations tailored to specific ecological scenarios can allow a high degree of understanding in the research questions that are associated with these scenarios (see [38] for the analysis of an insightful, though topically very different, example). Such an approach is pursued in chapter 5 for the specific scenario of optimal oviposition in the orange tip butterfly (*Anthocharis cardamines*).

1.4 The role of environmental variation

Environmental variation plays a central role in insect oviposition. For instance, how should insect oviposition strategies adapt to host availabilities that change between seasons and between habitat patches? Recent theoretical work by John McNamara and colleagues has supplied a useful conceptual foundation for examining the evolutionary effects of spatial and temporal variation in the environment [75]. This work is based on the old insight that reproduction is geometric in nature [36]. That is, members of a lineage reproduce in one season, their offspring in the next season, and so on—by this process, the reproductive success of each lineage is a multiplicative process, not an additive one. As a result, the measurement of choice when comparing fitnesses in spatio-temporally varying environments is the geometric, not the arithmetic mean [36, 75].

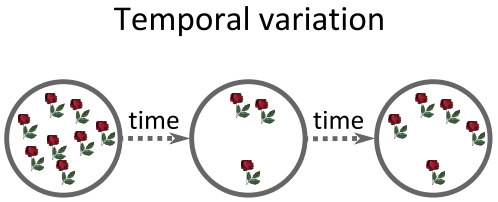
With reproduction being geometric in nature, environmental variation influences the adaptation of a lineage in different ways depending on whether this variation affects all lineage

members similarly, as in spatial variation, or individually, as in temporal variation. When faced with spatial variation, lineage members adapt primarily to conditions in patches with better-than-average environments—a phenomenon also known from studies of source and sink habitats (e.g. [44, 63]). Conversely, when faced with temporal variation, lineage members adapt primarily to conditions during seasons with worse-than-average environments. McNamara and co-workers call these phenomena "adaptive optimism" and "adaptive pessimism" [75].

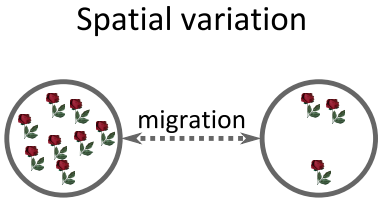
Adaptive optimism and pessimism arise because temporal and spatial environmental variation affect fitness in contrasting ways. Consider a scenario where host availability varies in space and time, and where different strains of insects either respond to these changes or do not do so. If host availability varies temporally, then insects reproducing at a constant but lower level often have higher reproductive success than insects benefiting from the good but also suffering during the bad seasons. This is because the geometric nature of reproduction makes decreased reproductive success in worse-then-average years particularly effective at lowering geometric mean fitness, simply because strain numbers are greatly reduced also in subsequent seasons following a particularly bad year. If host availability varies spatially, however, then insects reproducing at a constant but lower level in both patches often have lower reproductive success than insects benefiting from the good but also suffering in the bad patch. This is because, even if migration rates are high, a significant proportion of offspring produced in a good patch will stay within this good patch, which makes it profitable for lineages to adapt to better-than-average patches. As a result, insects in temporally varying environments are adaptively pessimistic and adapt to worse-than-average conditions, whereas insects in spatially varying environments are adaptively optimistic and adapt to better-then-average conditions. Figure 1.4 gives a schematic illustration for this line of argumentation.

As the concepts of adaptive optimism and pessimism illustrate, the role of environmental variation in strategic insect oviposition is two-fold. On the one hand, spatial variation in host availability will usually lead to insects adapting their oviposition strategies primarily to patches where host availability is higher than average—i.e., patches with lots of preferred hosts—rather than patches where preferred hosts are less common. Consider a scenario, for instance, where higher-quality hosts are common in some but rare in other patches, whereas lower-quality hosts are common in all patches. In this case, generalist oviposition strategies that include lower-quality hosts may still be less successful than specialist strategies that exploit only the high-quality host, even if these specialists have low reproductive success in patches where high-quality hosts are rare. This approach to the role of spatial heterogeneity is examined in detail in chapter 4.

Temporal variation in host availability, on the other hand, is expected to lead to insects adapting their oviposition strategies primarily to conditions when hosts are less common than average—i.e. seasons with few preferred hosts—rather than to conditions when preferred hosts are more common. Consider a scenario, for instance, where higher-quality hosts are common in some but rare in other years, whereas lower-quality hosts are common in all years. In this case, generalist oviposition strategies that include lower-quality hosts may produce higher fitness returns than specialist strategies that only exploit higher-quality hosts. Such generalist responses to temporal variation would correspond to bet-hedging strategies with lower-quality hosts acting as safeguards against not encountering sufficient acceptable hosts in particularly bad seasons. As is a partial focus of chapter 5, however, whether temporal variation indeed leads to generalism depends on the quantitative details of the system under



	Fitness			Total
	year 1	year 2	year 3	offspring
Strain A	10	2	9	180
Strain B	7	7	7	343



		Fitness			Total
		year 1	year 2	year 3	offspring
Strain A	Patch 1	10	10	10	833
	Patch 2	4	4	4	
Strain B	Patch 1	7	7	7	686
	Patch 2	7	7	7	

Figure 1.4. Temporal and spatial environmental variation can have differential effects on fitness. This phenomenon is illustrated here for the effects of variation in host availability on insect reproductive success. These numerical examples demonstrate how reproduction suffers disproportionately in lower-than-average years under purely temporal variation, whereas reproduction benefits disproportionately in higher-than-average patches under purely spatial variation. Observe that all strains have equal arithmetic but different geometric mean fitness. In the spatial case, migration rates are set to 0.5.

study.

These findings illustrate how, in general, the accuracy of environmental cues takes on a central role in questions on the evolution of insect strategic responses to oviposition decision problems. An old insight suggested that herbivorous insects confronted with more predictable resources are likely to be more specialist in their oviposition strategies, whereas those confronted with less predictable resources are likely to be more generalist [31]. Many exceptions exist to this rule, in part with patterns unrelated to resource predictability—such as butterflies feeding on herbaceous plants tending to be more specialist than those feeding on shrubs and trees (already noted in [31]). As the results highlighted above illustrate, however, what matters for the evolution of insect oviposition strategies in general is not whether resources are unpredictable at all, but whether this unreliability occurs in time or in space.

1.5 Outlook: Tackling the challenges of strategic oviposition

This thesis takes a multi-faceted approach to examining the evolutionary responses of insects to the challenges of strategic oviposition. Its focus lies on phytophagous insects, especially butterflies, where large amounts of empirical data are available. Generally, the research presented here aims at a greater understanding of the evolutionary processes that produce strategic oviposition preferences within the wider context of the evolutionary ecology of the specialism-generalism dichotomy.

The resulting research can be divided into four parts which I will introduce in turn. The

first two parts deal with basic processes underlying insect oviposition, namely how an individual's lifetime and its number of eggs limit its reproduction, how these limitations arise evolutionarily, and how they affect optimal oviposition strategies. The second two parts focus on two approaches to the evolution of generalism from specialism. First, I examine the potential of spatial heterogeneity to explain the evolution of generalism. Second, I assess the role of phenological specialization and temporal variability in producing generalist oviposition strategies.

1.5.1 Why do insects run out of eggs?

The first part of this thesis deals with the puzzling question of why insects often run out of eggs during their lifetime, a phenomenon known as egg limitation. After all, not having enough eggs to oviposit on all suitable encountered hosts may seem suboptimal from a maximizing-reproductive-success point of view. Previous theoretical work demonstrated, however, that a trade-off between investment in survival and reproduction can lead to the evolution of oviposition strategies with significant levels of egg limitation [93]. In essence, if insects invested more resources in eggs, their life spans would decrease and they could thus often not lay these eggs, which would render the investment unprofitable. This result sparked a lively debate on the importance of egg and time limitation in optimal insect oviposition [28, 94, 103].

In chapter 2 of this thesis, I reevaluate this debate on the evolution of time and egg limitation, taking into account various trade-off shapes and parameter settings. The presented results demonstrate that said debate was largely a discussion on assumptions and parameters, which left untouched the basic result that egg limitation results from a trade-off between survival and reproduction. In fact, my results show that a large range of evolutionarily stable levels of egg limitation can be reached, depending critically on the shape of the underlying trade-off as well as its parameters. As a result, this chapter suggests that the importance of egg and time limitation for optimal oviposition is likely to vary between species, and that neither of these factors can safely be ignored when examining strategic insect oviposition.

1.5.2 Can time and egg costs help explain strategic insect oviposition?

The second part of this thesis takes a different perspective on the importance of time and eggs for strategic insect oviposition. Specifically, this section analyses whether the opportunity costs associated with different oviposition strategies can be used to determine which strategies are most successful evolutionarily. This research was motivated by past work of Jay Rosenheim that compartmentalized the cost of oviposition into opportunity costs mediated by eggs and by time because, simply put, eggs that are laid now cannot be laid on potentially better hosts in the future, and time used for oviposition now cannot be used to find potentially better hosts in the future [94]. Thereby, the author aimed to show that eggs are more important for oviposition than the incidence of egg limitation would suggest because egg-mediated costs are very high.

As chapter 3 shows, the argument based on differential time and egg costs of reproduction as presented in [94] is flawed both quantitatively and conceptually. Quantitatively, the author disregards the time spent searching for new hosts in his calculation of costs mediated by time which, as a correction shows, leads him to overestimate the relative contributions of egg costs to the total cost of oviposition. Conceptually, and more importantly, these schematic time and egg costs do not correspond to the marginal fitness costs and benefits of different

oviposition strategies as calculated from a straightforward analytical model of oviposition. As a result, when aiming to assess the importance of time and eggs for optimal insect oviposition, model-based approaches to optimal oviposition may provide more productive techniques than schematic considerations of opportunity costs.

1.5.3 Can spatial heterogeneity favor generalist oviposition strategies?

The third part of the thesis returns to the question of the evolution of generalism in the context of strategic insect oviposition. Generalism is rare in phytophagous insects, and most species use only few host plant species for oviposition [60, 84, 116]. Since many host switches have occurred over evolutionary time, however, lineages are likely to have repeatedly widened their host niche breadths temporarily to both old and new hosts and subsequently have re-specialized on the new hosts [53–55]. As a result, generalist oviposition strategies must have evolved repeatedly from specialist strategies.

Since new host species are likely to be less suitable for larval development than ancestral ones because insects are better adapted to ancestral than to novel hosts, the emergence of generalism is not easily explained evolutionarily. A core theme of previous approaches to solving this question lies in the reliability of resources—if insects face less reliable resources, they are likely to become more generalist [31]. This idea, however, does not take into account the source-sink dynamics that may result from spatially unreliable resources and that may interfer with generalist evolutionary responses to such unreliabilities (e.g. [63]). As a result, the interplay between locally adaptive strategies and emergent source-sink dynamics between patches of different habitat quality represents a promising question when studying the evolution of phytophagous insect oviposition.

Specifically, I examine in chapter 4 whether the absence of preferred, high-quality hosts in certain patches within a metapopulation can induce insects to adopt more generalist oviposition strategies that also include previously unpreferred, low-quality hosts which are present in all patches. To this end, I employ a two-sided approach that consists of straightforward optimization models and more complex population genetic models. My results demonstrate that, while the optimization models predict that insects fare best if they respond to spatial heterogeneity by becoming more generalist, the same result does not arise in the population genetic model. This is because, when reproductive success varies spatially, organisms tend to adapt more to patches where reproductive success is high—i.e., they adapt to population sources, not to population sinks (see [44, 75]). As a result, this chapter suggests that spatial heterogeneity alone is unlikely to be an explanation for the evolution of generalism.

1.5.4 Can phenotypic specialization lead to generalist oviposition strategies?

What then can induce the evolution of generalism in ovipositing insects? Though presented in a much more general context, previous theoretical work suggests that temporal variation in resource availability may provide the key to why female phytophagous insects include host plants in their diet breadth that are suboptimal for their larvae [75]. In essence, females may use suboptimal hosts as safeguards against not laying sufficient eggs in times when high-quality hosts are absent.

As a result, examining how the temporal availability of suitable hosts shapes the oviposition preferences of female phytophagous insects may represent an insightful approach to the evolution of insect oviposition strategies. While this approach has been suggested verbally in

the discussion of empirical findings(see [127]), to my knowledge no theoretical models exist that explicitly assess its validity.

The fourth part of the thesis therefore examines how temporal patterns of host availability affect strategic oviposition, using as an example the orange tip butterfly, *Anthocharis cardamines*. This butterfly represents an interesting case study: On the one hand, its larvae are phenological specialists in that they do not eat leaves but instead feed primarily on their host plants' seeds. On the other hand, adult females show a comparably wide diet breadth, using for oviposition a number of cruciferous plant species.

Chapter 5 examines the hypothesis whether the orange tip larvae's phenological specialism has led to the evolution of the adult females' oviposition generalism [127]. With this purpose, I develop an individual-based simulation model of oviposition in phytophagous insects that is tailored to the situation of the orange tip butterfly. The simulation results confirm the hypothesis that phenological specialism can entail oviposition generalism, likely due to a corresponding decrease in perceived host availability. Moreover, the simulation results demonstrate that competition of surviving larvae on different host species may play a larger role in optimal oviposition than larval survival *per se* as resulting from differential larval performance on different hosts. With regard to empirical questions of strategic insect oviposition, the simulation results give a number of specific research impulses that could be pursued in the future. Moreover, due to its modular nature, the simulation model could be expanded and applied to other specific research questions, both theoretical and empirical, that are discussed in detail.

1.5.5 Conclusion: Theoretical approaches to strategic oviposition

Taken together, the results presented in this thesis demonstrate the versatility of different theoretical approaches to examine questions of strategic oviposition in insects. Empirical results demonstrate a large range of variation in oviposition behaviors, even on very general scales. For instance, sometimes genetically isolated populations diverge in their oviposition preferences, but sometimes ancestral preferences are retained [106, 111]; and sometimes oviposition preferences are in accord with larval performance, but often they are not [39]. As the different sections of this thesis demonstrate, these divergent patterns can be the result of underlying physiological factors such as trade-off shapes or parameters (chapters 2 and 3), but can also be due to spatio-temporal variation of environmental factors such as host availability (chapters 4 and 5).

As a result, such theoretical models as are developed in this thesis offer insights into why insects have evolved to lay their eggs the way they do; insights which would hardly have been available from empirical data alone. In the future, combining these models with detailed empirical work sufficient to parametrize them, as well as to check their predictions, may present a productive approach towards a deeper understanding of strategic insect oviposition (see chapter 6).

2 A strategic argument for the evolutionary significance of egg limitation in insect oviposition

Chapter summary

Ovipositing insects can be limited in their egg-laying strategies both by the time available and by the number of eggs they carry. Since insects neither are immortal nor carry an infinite number of eggs, both egg and time limitation are likely to influence lifetime reproductive success and jointly shape oviposition behavior. Evolutionarily, egg limitation has been shown to arise from a trade-off between survival and reproduction. Previous studies, however, have debated the significance of egg limitation for optimal oviposition strategies while making different assumptions about the underlying life-history trade-off. In order to examine this question in detail, I develop a straightforward model of insect oviposition with endogenous egg and time limitation that considers three different trade-off shapes between mortality and egg number—hyperbolic, linear, and sigmoidal. This model shows that all three trade-off shapes lead to optimal oviposition strategies that may contain considerable egg limitation risks of up to 50%. Additionally, I show that a model-version ignoring egg limitation can significantly underestimate reproductive success and overestimate optimal reproductive investment. These results highlight the importance of egg limitation for evolutionary analyses of optimal insect oviposition.

2.1 Introduction

As in all iteroparous organisms, reproduction in insects is constrained by a fundamental trade-off between current and future reproduction, where investing more resources into current reproduction carries the cost of reduced future reproduction [4]. This trade-off results from the strategic allocation of finite resources between investment into survival and investment into reproduction[57]. In insects, the cost of reproduction therefore manifests as a trade-off between an individual's number of eggs and its life span [56].

The exact shape of the trade-off between survival and reproduction in insects remains unclear. Early modeling work assumed a linear relationship between mortality rate and investment in reproduction [93] which, given exponentially distributed lifetimes, translates to a hyperbolic relationship between life span and number of eggs. Since this assumption implies varying fecundity costs in terms of reduced life span per additional egg, however, later works preferred a linear relationship between life span and number of eggs—i.e., a hyperbolic trade-off between mortality and egg number—where life span is reduced equally by each additional egg [103]. The two insect case studies that exist support such a linear relationship between life span and egg production [27, 109], and this assumption has become the status-quo in most recent modeling work (e.g. [95, 97], but see [33]). Earlier empirical

data on rotifers and fish, however, do not give more support to a linear relationship between life span and reproduction compared to a hyperbolic one [4]. Assuming a wider range of trade-off shapes thus represents a more conservative approach when examining insect oviposition strategies, especially since trade-off shapes may markedly influence optimal oviposition and resource allocation strategies (see below and [27]).

Regardless of its shape, the trade-off between life span and egg production needs to be examined in the context of oviposition strategies evolved to maximize lifetime reproductive success. A specific female insect's reproductive success, however, will always be limited either by her lifetime, so-called *time limitation*, or by the number of eggs she carries, so-called *egg limitation*. If a female dies before laying all her eggs, her reproduction was limited by the time available and she is called "time-limited"; if she dies after laying all her eggs, her reproduction was limited by the number of eggs available and she is called "egg-limited" (refer back to figure 1.1 on page 3 of chapter 1). However, each oviposition decision alters the probabilities of becoming egg- or time-limited because choosing to lay an egg increases the risk of egg and decreases that of time limitation whereas rejecting a potential host for oviposition does just the opposite (refer back to figure 1.2 on page 4 of chapter 1). Each oviposition decision thus influences the fitness costs and benefits of the underlying oviposition strategy. As a result, time and egg limitation are outcomes of strategic oviposition.

The relative importance of egg and time limitation for optimal insect oviposition strategies has been the subject of some recent debate. In essence, this debate focuses on the assumptions under which egg and time limitation arise from the trade-off between life span and egg production. These assumptions relate to the shape of the trade-off (see above) as well as the extent of spatial and temporal stochasticity in host availability.

First, assuming a hyperbolic trade-off between life span and egg number as well as stochasticity only in survival, Rosenheim [93] argued for a central role of egg limitation in insect oviposition strategies. A group of other researchers [27, 28, 103] then questioned this large influence of egg limitation because Rosenheim's high levels of egg limitation were a result of his, to their eyes, invalid hyperbolic trade-off assumptions and because, additionally, temporal stochasticity in host availability reduced the incidence of egg limitation. Recent theoretical work by Rosenheim and colleagues [95]—now also assuming a linear trade-off between life span and egg production—demonstrated that, however, considering not only temporal but also spatial stochasticity in host availability again leads to an increase in the incidence of egg limitation. Moreover, the authors showed that, though most females remain time-limited, a disproportionately large amount of eggs is laid by females destined to become egg-limited, which they interpreted as increasing the importance of egg limitation.

In summary, while egg and time limitation clearly result from a trade-off between survival and reproduction, the exact shape of this trade-off remains unclear, and along with it the extent of egg and time limitation as well as their influence on optimal oviposition strategies. In this chapter, I return to the basic question of how the functional shape of the trade-off influences the significance of egg and time limitation for optimal oviposition strategies. Assuming linear, hyperbolic and sigmoidal relationships between mortality and egg number, I show that these different trade-off shapes and their various parameter settings can produce evolutionarily stable incidences of egg and time limitation ranging from 0% to 50%. Assumptions on trade-off shape and parameters are therefore critical when assessing strategic insect oviposition behavior. Moreover, I derive a measure of the evolutionary significance of egg limitation from my model. I find that, across all trade-off shapes and for most parameter settings, models that do not consider egg limitation would significantly underestimate fitness

and overestimate optimal reproductive investment. These findings highlight the importance of egg limitation for evolutionary analyses of optimal insect oviposition.

2.2 Model

I model the oviposition of a proovigenic insect species—i.e., a species that ecloses from its pupa with its full egg complement and does not produce additional eggs during its lifetime—that lays eggs on only one host plant species. I derive a formula for the insect's lifetime reproductive success as a function of its number of eggs at eclosion, presupposing neither egg nor time limitation. In order to estimate optimal egg numbers, I maximize this formula assuming a suite of differently shaped life history trade-offs between mortality and reproductive investment. Finally, I reenter this optimal egg number into my oviposition model to determine the corresponding, fitness-maximizing risk of egg limitation as well as the ecological and evolutionary importance of egg limitation for optimal oviposition.

2.2.1 Lifetime reproductive success

In my model of insect oviposition, females lay one egg per time period, survive to another period with probability q, and carry n eggs at eclosion. Female thus become egg-limited with probability q^n and time-limited with complement probability $1 - q^n$.

I calculate the expected number of eggs Y laid by a female as the sum of her laying all n eggs weighted with the probability of egg limitation, q^n, and the expected value of her laying less than n eggs weighted with the probability of time limitation, $1 - q^n$.

$$\mathrm{E}(Y) = n \cdot q^n + \mathrm{E}(Y|Y < n) \cdot (1 - q^n) \tag{2.1}$$

Given that the probability that a given female lays exactly k eggs is $\mathrm{P}_k = q^k \cdot (1 - q)$, and that the probability of laying less than n eggs is the probability of time limitation, $1 - q^n$, I can calculate the expected number of eggs laid by a time-limited female laying as:

$$\begin{aligned} \mathrm{E}(Y|Y < n) &= \sum_{l=0}^{n-1} l \cdot \mathrm{P}(Y = l|Y < n) = \sum_{l=0}^{n-1} l \cdot \frac{\mathrm{P}(Y = l \wedge Y < n)}{\mathrm{P}(Y < n)} \\ &= \sum_{l=0}^{n-1} l \cdot \frac{\mathrm{P}(Y = l)}{\mathrm{P}(Y < n)} = \sum_{l=0}^{n-1} l \cdot \frac{q^l (1 - q)}{1 - q^n} \\ &= \frac{1 - q}{1 - q^n} \sum_{l=0}^{n-1} l \cdot q^l \end{aligned} \tag{2.2}$$

I calculate the right-hand sum by rewriting it as the derivative of another sum, deriving a formula for that sum, and differentiating this formula, which gives for the sum $\sum_{l=0}^{n-1} l \cdot q^l = q\frac{(n-1)q^n - nq^{n-1} + 1}{(1-q)^2}$. The expected number of eggs laid by a time-limited female as derived in equation 2.2 thus becomes:

$$\mathrm{E}(Y|Y < n) = \frac{q - nq^n + (n-1)\, q^{n+1}}{(1 - q^n)(1 - q)} \tag{2.3}$$

I resubstitute this result into equation 2.1 and arrive at the expected number of eggs Y

laid by any female.

$$\begin{aligned} \mathrm{E}(Y) &= q^n \cdot n + (1 - q^n) \cdot \mathrm{E}(Y | Y < n) \\ &= nq^n + \frac{q - nq^n + (n-1)\, q^{n+1}}{1 - q} = \frac{q\,(1 - q^n)}{1 - q} \end{aligned} \tag{2.4}$$

If I approximate a female's fitness as the number of eggs she lays, then this equation represents the female's fitness function. I therefore maximize this function over the size of a female's egg complement n to determine the optimal oviposition strategy.

2.2.2 Survival probabilities

In order to calculate a females reproductive success, I need to specify the probability q of surviving to lay another egg. This probability is the complement of the probability of dying before another egg is laid, which is equal to the mortality rate divided by the sum of oviposition rate and mortality rate.

$$q = 1 - \frac{\text{Mortality rate}}{\text{Mortality rate} + \text{Oviposition rate}} \tag{2.5}$$

To estimate q, I need to specify both mortality and oviposition rates. I take the mortality rate μ to be constant over an insect's lifetime, thus assuming mortality to be random, uncorrelated with oviposition, and without aging effects. Constant mortality rates let life spans be exponentially distributed (with mean life span $\overline{L} = \frac{1}{\mu}$) as has been assumed in a number of previous theoretical studies (e.g. [33, 48, 93, 121]). I then derive oviposition rates from the rates of encounter with suitable hosts and these host species' rates of acceptance by ovipositing insects. Since only one host species is present in my case and should thus always be accepted for oviposition, oviposition rates are equal to the rate f with which insects encounter this host. Altogether, I can represent the probability of surviving to lay another egg as:

$$q = 1 - \frac{\mu}{\mu + f} = \frac{f}{\mu + f} \tag{2.6}$$

2.2.3 Fitness function

Entering the results of equation 2.6 into equation 2.4 lets us determine a female's expected lifetime reproductive success, the number of eggs she can lay in her lifetime, as a function of host encounter rate f, mortality rate μ, and her number of eggs at eclosion n:

$$\mathrm{E}(Y) = \frac{\frac{f}{\mu+f}\left(1 - \left(\frac{f}{\mu+f}\right)^n\right)}{\frac{\mu}{\mu+f}} = \frac{f}{\mu}\left(1 - \left(\frac{f}{\mu + f}\right)^n\right) \tag{2.7}$$

The structure of this fitness function corresponds to a female insect's maximal potential rate of reproduction—her oviposition rate divided by her mortality rate—multiplied with her risk of not being able to achieve this potential because she becomes time-limited:

$$\text{Fitness} = \frac{\text{Oviposition rate}}{\text{Mortality rate}} \cdot \text{Risk of time limitation} \tag{2.8}$$

Calculations were done by hand and in Mathematica 8.0.1 (Wolfram Research, Inc.); maximizations could not be done analytically and were therefore performed numerically in R v 2.13.2 (R Development Core Team, 2011) using RStudio 0.95.262 (RStudio, Inc., 2011).

2.3 Results

2.3.1 Persistent risks of egg limitation

In my model, an insect's optimal oviposition strategy consists of exactly that number of eggs at eclosion n which maximizes the expected number of eggs a female can lay during her lifetime Y, as determined by the fitness function of equation 2.7. Since this fitness function rises monotonically with n, it follows trivially that the largest possible egg number will deliver the highest reproductive success. However, this finding holds only in the absence of trade-offs between survival and reproduction.

The three different trade-off shapes

I implement the life-history trade-offs between survival and reproduction as a dependency between mortality rate and the number of eggs at eclosion using three different functional shapes with two parameters each. First, I let mortality rates scale hyperbolically with egg number, depending on a total resource level T and a scaling parameter a_H. This corresponds to the linear relationship between life span and reproductive investment assumed by most recent modeling studies (see introduction). Second, I scale mortality linearly with egg number, depending on a baseline mortality a_L and a growth rate parameter b_L. Apart from the newly-added baseline mortality, this corresponds to the trade-off used in the first model on the evolution of egg limitation [93]. Third, I let mortality rates scale sigmoidally with egg number, depending on a parameter m setting the position of maximum growth and a growth rate parameter b_S.

The choice of trade-off shape has consequences for maximum possible egg numbers and mean life spans. These characteristics as well as the trade-offs' functional forms and parameter settings are summarized in table 2.1. Necessarily, these three trade-offs produce differently shaped relations between life span and egg number, which are illustrated in figure 2.1. To ensure comparability of results, I chose parameters so that the different trade-off shapes span roughly the same parameter space for mean life spans between 0 and 50 as well as egg numbers between 0 and 150 (figure 2.1). As in previous studies [93, 103], host encounter rates were varied between 0.1 and 20.

Qualitatively, the main difference between the three trade-off shapes lies in how each trade-off's parameters affect mean life span at its maximum, i.e. when insects invest nothing in reproduction, and at its minimum, i.e. when insects have reached the maximum number of eggs. Maximum life span is fixed for the linear trade-off at the reciprocal of the trade-off's absolute parameter a_L, irrespective of the scaling parameter b_L, but depends on *both* parameters in the two other trade-off shapes. Minimum life span is fixed to zero when insects reach their maximum egg number T in the hyperbolic trade-off, irrespective of the trade-off's other parameter a_H, but always depends on *both* parameters in the two other trade off shapes (where minimum life span never reaches zero and there thus exists no pre-defined maximum egg number—see bottom of table 2.1 and figure 2.1).

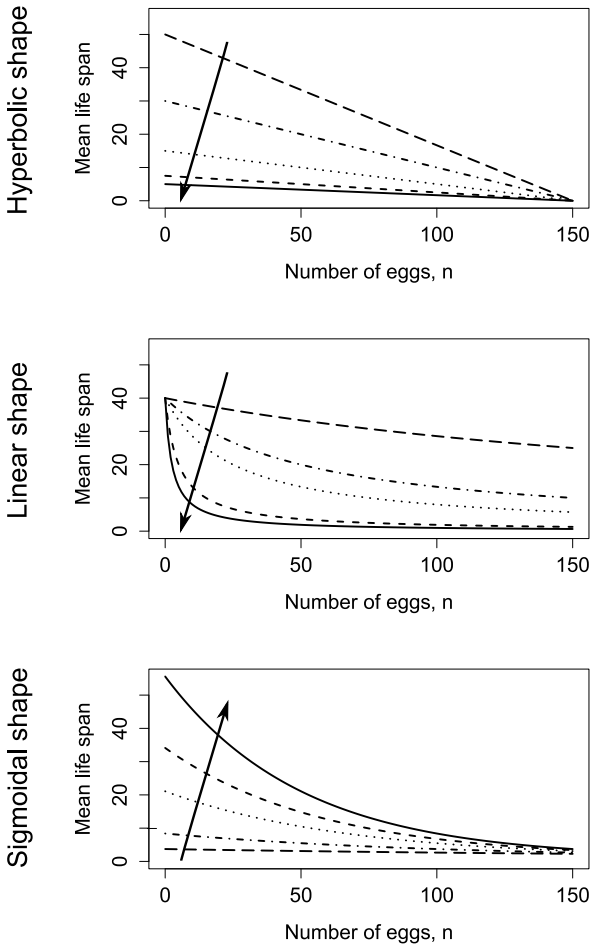


Figure 2.1. Differently shaped trade-offs produce varying relationships between life span and reproduction. Shown are the relationships between a female's life span and the number of eggs she carries at eclosion as generated by the model's three different trade-off shapes between mortality and egg number—hyperbolic, linear, and sigmoidal. Parameters are set and varied for each trade-off shape as specified in table 2.1 with growth rate parameters a_H (hyperbolic, top panel), b_L (linear, mid panel), and b_S (sigmoidal, bottom panel) increasing in the direction of the arrows. That is, a_H is set to 3, 5, 10, 20, and 30 with $T = 150$ for the hyperbolic trade-off; b_L is set to 0.0001, 0.0005, 0.001, 0.005, and 0.01 with $a_L = 0.025$ for the linear trade-off; and b_S is set to 0.005, 0.01, 0.015, 0.0175, and 0.02 with $m = 200$ for the sigmoidal trade-off.

Table 2.1. Details of the three different trade-off shapes used in the model, their parameters, and their characteristics. Average life spans, $\overline{L}$, are calculated as the reciprocal of mortality rates μ.

	Trade-off shapes		
	Hyperbolic	Linear	Sigmoidal
Functional forms	$\mu = \frac{a_H}{T-n}$ $\overline{L} = \frac{T-n}{a_H}$	$\mu = a_L + b_L n$ $\overline{L} = \frac{1}{a_L + b_L n}$	$\mu = \frac{1}{1+e^{-b_S(n-m)}}$ $\overline{L} = 1 + e^{-b_S(n-m)}$
Parameter settings	$T = 150$ $a_H \in (3; 30)$	$a_L = 0.025$ $b_L \in (0.0001; 0.01)$	$m = 200$ $b_S \in (0.005; 0.02)$
Range of possible mean life spans	For minimal a_H: $\overline{L}_{n=0} = 50$ $\overline{L}_{n=100} = 16.\overline{6}$ $\overline{L}_{n=150} = 0$ For maximal a_H: $\overline{L}_{n=0} = 5$ $\overline{L}_{n=100} = 1.\overline{6}$ $\overline{L}_{n=150} = 0$	For minimal b_L: $\overline{L}_{n=0} = 40$ $\overline{L}_{n=100} = 28.6$ $\overline{L}_{n=150} = 25$ For maximal b_L: $\overline{L}_{n=0} = 40$ $\overline{L}_{n=100} = 0.98$ $\overline{L}_{n=150} = 0.66$	For minimal b_S: $\overline{L}_{n=0} = 3.72$ $\overline{L}_{n=100} = 2.65$ $\overline{L}_{n=150} = 2.28$ For maximal b_S: $\overline{L}_{n=0} = 55.6$ $\overline{L}_{n=100} = 8.39$ $\overline{L}_{n=150} = 3.72$
Number of eggs, n	Limited to T	Unlimited	Unlimited
$\overline{L}(n = 0)$	Varies with a_H	Fixed for all b_L	Varies with b_S
$\overline{L}(n = T)$	Fixed for all a_H	Varies with b_L	Varies with b_S

Effects of trade-offs on fitness and egg limitation

Including a trade-off between survival and reproduction lets the fitness function of equation 2.7 reach a peak at an intermediate number of eggs, n. As expected, this value decreases with increasing effect of egg number on life span, as modulated by the respective trade-off's growth rate parameter (see figure 2.2, left column). The risk of egg limitation, while naturally decreasing with the number of eggs at eclosion, also shrinks with increasing growth rate parameters (see figure 2.2, right column).

For each parameter setting in each trade-off shape and for each host encounter rate, I determine the optimal number of eggs at eclosion by numerically maximizing the fitness function of equation 2.7 over all n. I then calculate the risks of egg and time limitation produced by this optimal strategy. Depending on parameter choice, these optimal oviposition strategies contain considerable risks of egg limitation, varying between 0% and 50%, that rise with increasing host encounter rates (see figure 2.3, left column).

The scope of evolutionarily stable egg limitation levels is similar across all three parameter shapes. Egg limitation risks increase with scaling parameter a_H for the hyperbolic trade-off but decrease with growth rate parameters b_L and b_S in the linear and sigmoidal cases. For the hyperbolic trade-off with baseline mortality a_H set to zero, my model resembles the results of Rosenheim [93] in that egg limitation is largely independent of host encounter rates (data not shown). This finding, however, no longer holds once even a small baseline mortality is introduced (e.g., 2.5% in figure 2.3) and may thus have been an artifact of

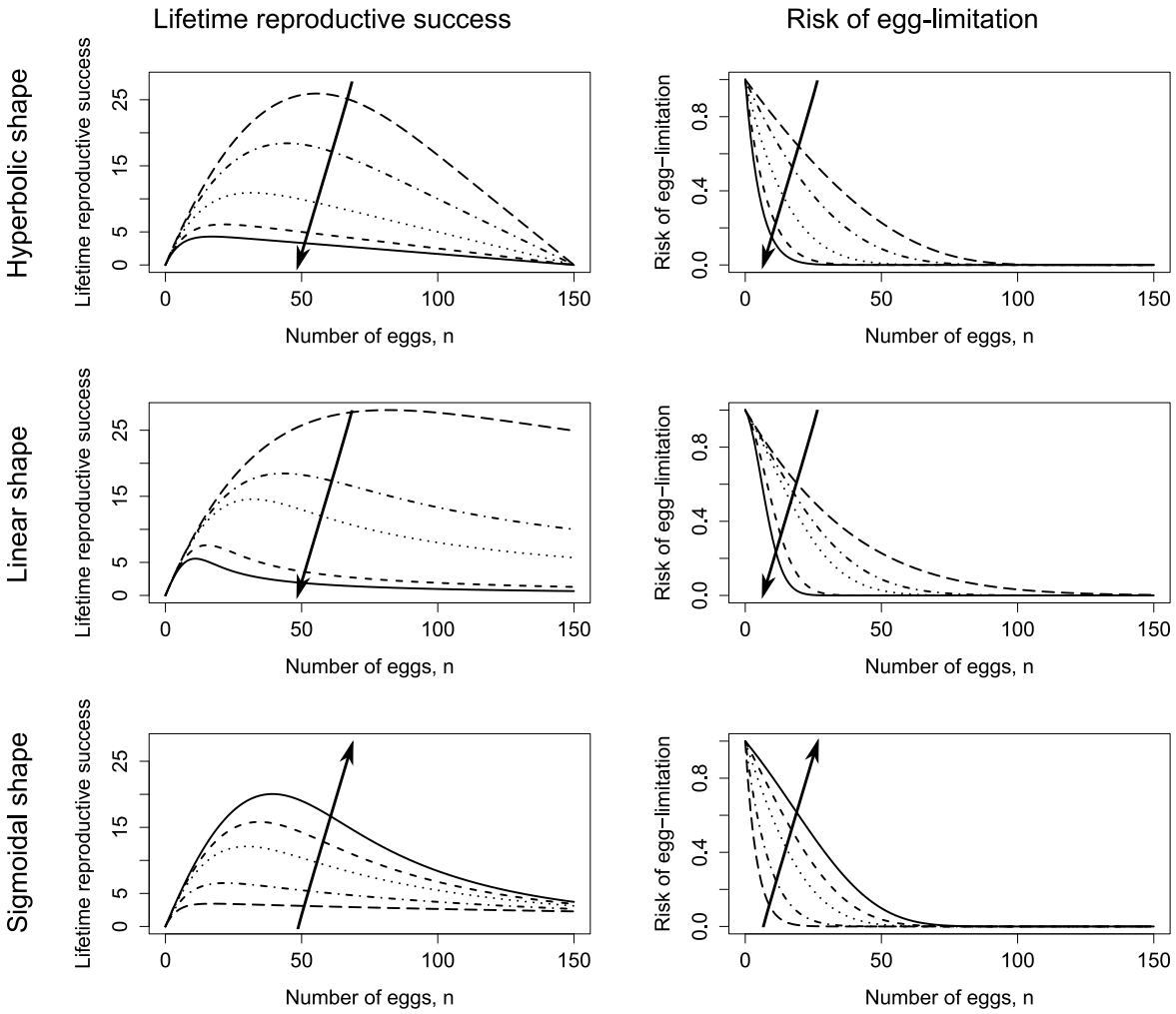


Figure 2.2. Lifetime reproductive success and risk of egg limitation as functions of egg number. Shown are exemplary response curves for lifetime reproductive success (left column) and risk of egg limitation (right column) as a function of the number of egg at eclosion, n, for the model's three different trade-off shapes between mortality and egg number—hyperbolic (top row), linear (mid row), and sigmoidal (bottom row). Host encounter rates are set to $f = 1$; other parameters are set as in figure 2.1 with growth rate parameters a_H (hyperbolic), b_L (linear), and b_S (sigmoidal) increasing in the direction of the arrows.

Rosenheim's original modeling structure where such a baseline mortality was absent. As expected, optimal egg numbers rise with increasing host encounter rates for all three trade-off shapes irrespective of scaling parameter choice (see figure 2.3, right column).

Consequences for strategic oviposition

My finding that oviposition is hardly ever limited only by eggs or only by time across the three different trade-offs demonstrates a more general problem in optimal oviposition: The number of eggs a female lays successfully in her lifetime is expected to be a product of the maximal rate of reproduction and the reduction due to time limitation (see equation 2.8). However, these two quantities usually cannot be regulated independently because changing one life history parameter will often increase reproductive success via one quantity but decrease it via the other. Increasing oviposition rates, for example, increases reproductive potential but decreases the probability of time limitation, while increasing egg number and mortality, as in my case, does just the opposite. As a result, I expect intermediate numbers of eggs at eclosion to often give highest fitness returns, so that optimal oviposition strategies contain considerable risks of both time and egg limitation (see section 2.4 and [96]).

2.3.2 Ecological importance of egg limitation

Rosenheim [95] suggested to use the proportion of eggs laid by females destined to become egg-limited as a measure of the ecological importance of egg limitation. In my model context, this measure corresponds to the relative fitness contribution of egg-limited females, i.e. the first term of the unsimplified equation 2.4 divided by the entire equation 2.4, with q set as in equation 2.6 and for each trade-off shape.

Analyzing the optimal oviposition strategies resulting from my model shows that, as expected, the relative fitness contributions of egg-limited females rise with host encounter rates. Moreover, these fitness contributions depend on the scaling parameters in the same manner as the optimal risks of egg limitation (figure 2.4). As a rule of thumb, the ecological importance of egg limitation is about twice as large as the evolutionarily stable risk of egg limitation (compare figure 2.3, left column).

2.3.3 Evolutionary importance of egg limitation

For evolutionary considerations, the fitness contributions of egg-limited females can be misleading as a measure for the impact of egg limitation on optimal oviposition strategies. Even though egg-limited females contribute more to fitness than the incidence of egg limitation would suggest, egg limitation does not rise in frequency. This is because egg limitation is not a strategy itself, but the result of an optimal oviposition strategy where a certain number of eggs at eclosion maximizes lifetime reproductive success but *also* leads to egg limitation. That is, increasing the risk of egg limitation could only be achieved by having more eggs which, however, would produce lower fitness returns.

As a result, a more insightful measure for the evolutionary importance of egg limitation are the relative inaccuracies between models considering only time limitation and those considering both time and egg limitation, regarding both the resulting fitness values and the resulting optimal reproductive investments. To derive such a measure, I maximize the expected number of eggs laid by a time-limited female (i.e., equation 2.3 with q set as in equation 2.6 for each trade-off shape), thereby creating a reduced model version that assumes

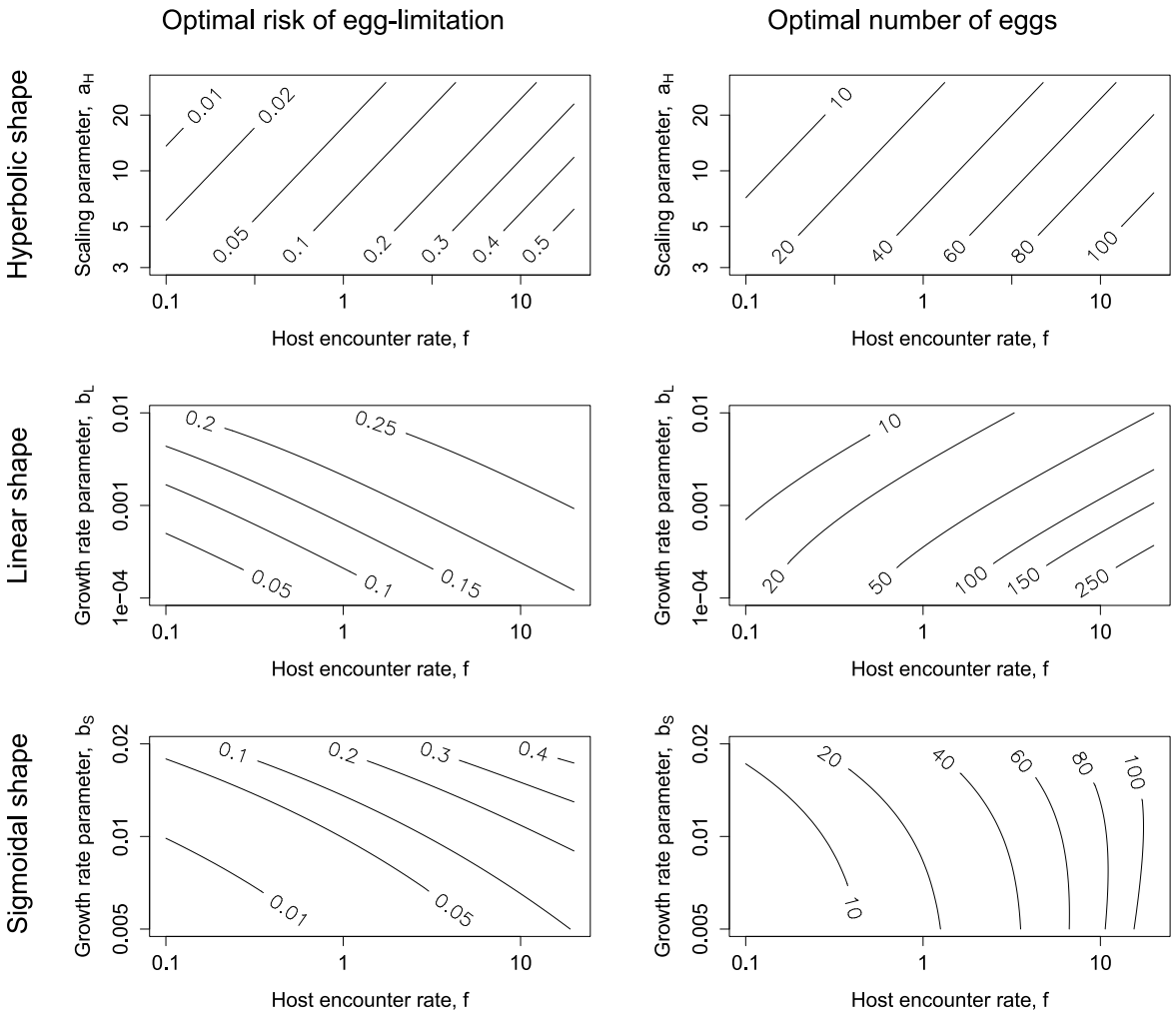


Figure 2.3. Life history trade-offs with varying shapes can lead to considerable risks of egg limitation. Shown are contour plots for a female's optimal risk of egg limitation (left column) at the optimal number of eggs that maximizes her lifetime reproductive success (right column) for the model's three different trade-off shapes between mortality rate and egg number—hyperbolic (top row), linear (mid row), and sigmoidal (bottom row). Optimal egg numbers are calculated by maximizing equation 2.7, risks of egg limitation by entering these results into equation q^n (see model section for details). Parameters are set and varied for each trade-off shape as specified in table 2.1.

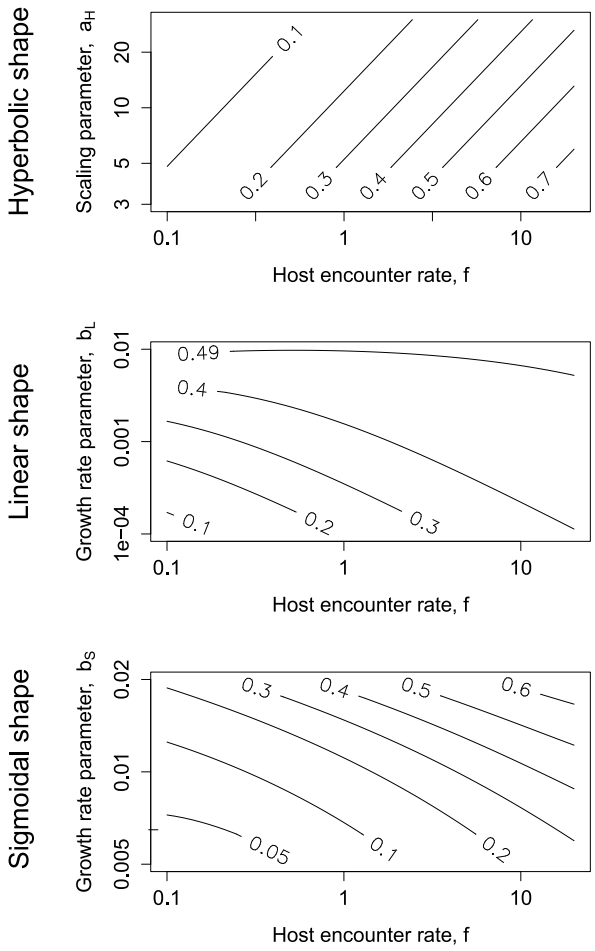


Figure 2.4. Ecological significance of egg limitation. Shown are contour plots for the ecological significance of egg limitation, i.e. the contributions of egg-limited females to lifetime reproductive success, for the model's three different trade-off shapes between mortality rate and reproduction—hyperbolic (top row), linear (mid row), and sigmoidal (bottom row). See results section for calculation details. Parameters are set and varied for each trade-off shape as specified in table 2.1.

all females to be time-limited. I subtract the resulting maximal lifetime reproductive success for strict time limitation from that of the complete model and, for normalization, divide by the latter term.

This approach shows that ignoring egg limitation may lead to significant fitness-underestimation of up to 35% across all trade-off shapes (see figure 2.5, left column). Quantitatively, this evolutionary importance of egg limitation is about equal to the evolutionarily stable risk of egg limitation and depends on parameters in the same manner (compare figure 2.3). In terms of evolutionary dynamics where fitness differences of few percent can have large effects, these relative inaccuracies are of significant size unless egg limitation is extremely rare. As a result, though a minority condition, egg limitation represents a influential factor when it comes to fitness estimations.

Moreover, I assess inaccuracies in optimal reproductive investment by dividing optimal egg numbers from the time limitation model by those from the complete model. This shows that ignoring time limitation leads to significant overestimation of optimal egg numbers across all trade-off shapes (see figure 2.5, right column). As a result, similar to the case of fitness estimations, egg limitation may only affect a fraction of all females but remains an important factor in evolutionary considerations of strategic insect oviposition.

2.4 Discussion

Ovipositing insects can be limited in their egg-laying strategies both by the time available and by the number of eggs they carry. Here, I develop a simple mathematical model of insect oviposition to examine why egg and time limitation arise in the first place. Taking a broader perspective than previous approaches, I assume three different shapes for the life history trade-offs between mortality and reproduction, hyperbolic, linear, and sigmoidal. Across these three trade-off shapes, optimal oviposition strategies arise that may contain considerable risks of egg limitation of up to 50%. Moreover, a version of my model that excludes egg limitation leads to significant underestimation of fitness and overestimation of optimal reproductive investment, which further highlights the importance of egg limitation for evolutionary considerations on optimal oviposition. In summary, my results strengthen the view that neither egg nor time limitation play negligible roles in shaping insect oviposition strategies, but that care should be taken regarding the underlying trade-off assumptions.

2.4.1 Adaptive egg limitation

As the model results show, egg limitation is adaptive in the sense that expected reproductive success would be lower if one, for example, decreased egg limitation and increased time limitation. This stands in contrast to previous work that suggested that, instead, egg limitation is something that should be avoided as long as hosts can still be encountered [27].

In the past, environmental stochasticity has been implicated in the evolution of egg limitation because it makes impossible the exact fit of an insect's life history parameters with the oviposition opportunities in its current environment (e.g. [94, 97]). Specifically, while temporal variation in oviposition opportunity was shown to decrease the incidence of egg limitation, spatial variation elevated egg limitation levels (see chapter introduction—[95, 103]). Such environmental variation, however, is entirely absent from my model, where stochasticity only results from exponentially distributed life spans. As a result, even in the absence of environmental variation, egg limitation often occurs at non-trivial levels and has a significant

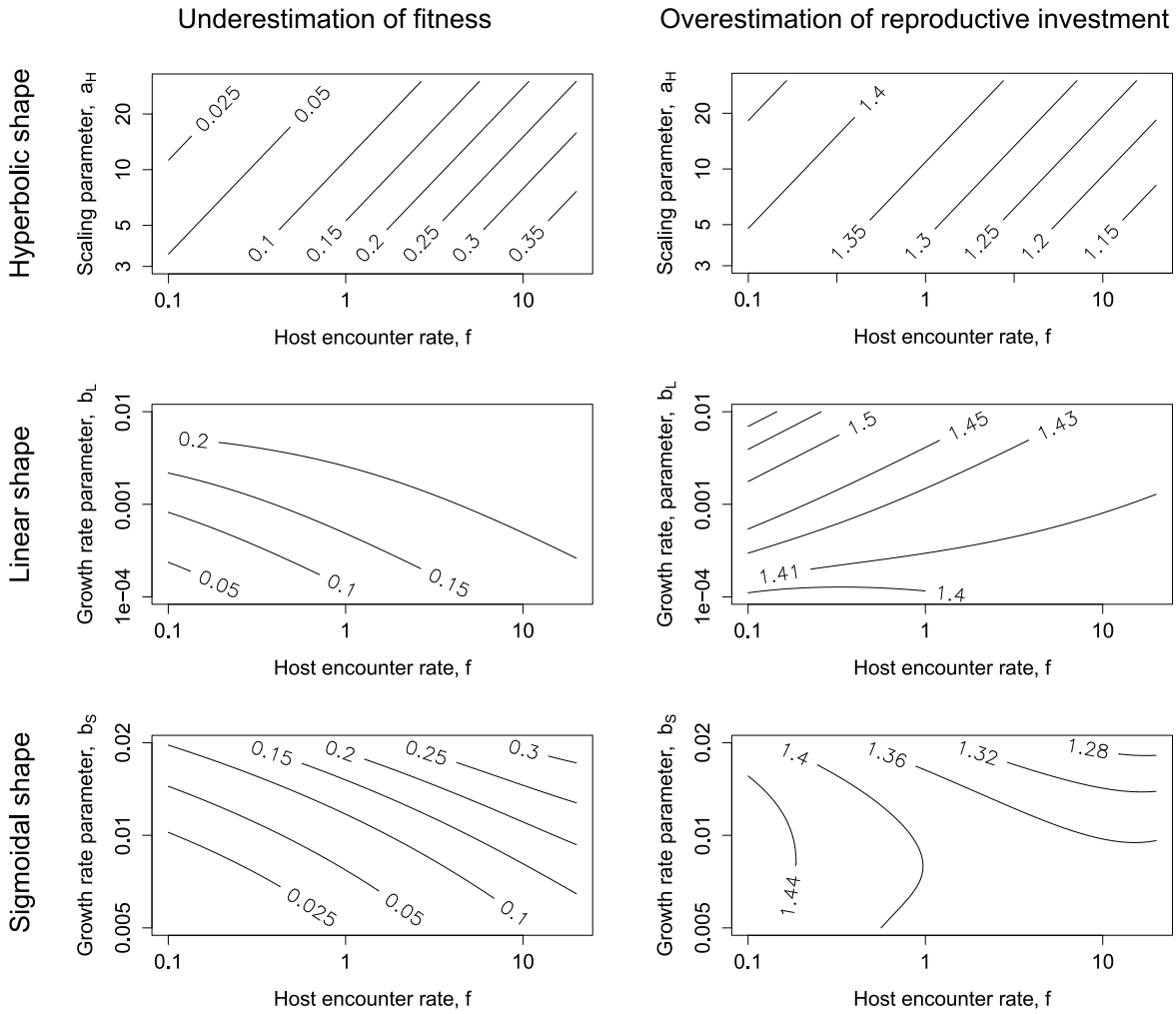


Figure 2.5. Egg limitation has high evolutionary significance because models ignoring egg limitation significantly underestimate fitness and overestimate optimal reproductive investment. Shown are contour plots for the relative underestimation of maximum lifetime reproductive success (left column) and for the relative overestimation of optimal egg number (right column) if one considers a model with only time limitation compared to one with both egg and time limitation (see results section for calculation details). These results are presented for model's three different trade-off shapes between mortality and reproduction—hyperbolic (top row), linear (mid row), and sigmoidal (bottom row). Parameters are set and varied for each trade-off shape as specified in table 2.1.

influence on evolutionary considerations of optimal oviposition.

2.4.2 Empirical comparisons

Empirical findings on the incidence of egg and time limitation are rare because it is usually difficult to measure the factors limiting reproductive success [121]. In some haplo-diploid parasitoids, the degree of egg and time limitation can be measured indirectly via the sex ratio [48]. In most cases, however, post-reproductive insects would have to be dissected and their ovaries examined to assess whether they were time- or egg-limited [97]. As a result, model-based approaches as the one presented here represent an important tool to assess the role of egg limitation in optimal oviposition.

The few available direct field measurements of the probability of egg limitation estimate this risk as between 7% and 17% [94, 97]. These estimates fall within the levels of egg limitation produced by my model for the different trade-off shapes and a relatively wide range of parameters. However, egg and time limitation levels can vary even within species depending on site and time of year [122], which weakens conclusions based on few measurements.

2.4.3 Strategic oviposition and host plant availability

A field study on the butterfly *Leptidea sinapis* estimates host plant availability to be the second most important factor constraining female fitness in the wild after temperature [5]. This study is especially relevant to the trade-off based modeling approach presented here because it shows that females differentially allocate resources to reproduction depending on their own body size, thereby reaching different optima for differently sized females [5]. While size differences were absent from my model, it is noteworthy that insects seem to possess an evolved program for resource allocation to reproduction that takes into account such ecological variables as host plant availability.

On a more general level, my model shows that higher host encounter rates lead to higher egg numbers across all trade-off shapes (fig.2.3, right column), which has been shown to be the case in a proovigenic parasitoid [56]. Finally, since smaller diet breadths lead to lower encounter rates of suitable hosts, my model predicts insects with smaller diet breadths to have higher life spans because of the trade-off between mortality rate and reproduction. Such negative correlations have indeed been found in female Lepidoptera [56].

2.4.4 Conclusion

In summary, the fact that optimal oviposition strategies usually contain a mix of egg and time limitation is an example of the principle that, when faced with several fitness-limiting factors, fitness-maximizing strategies are expected to balance these factors [96]. Thus, natural selection has molded insect life-histories to balance the limiting factors of eggs and time so that, in most cases, individuals are not only limited by one, but by both of these factors. The significance of *both* these limiting factors is highlighted by my finding that ignoring the rarer one, egg limitation, leads to significant mis-estimation of optimal insect oviposition strategies unless egg limitation is extremely rare. As a result, neither time nor eggs can safely be ignored in evolutionary considerations of insect oviposition. The strategic approach to optimal oviposition presented in this chapter may therefore help explain why egg limitation is a minority condition with major evolutionary consequences.

3 The role of time and egg costs in optimal oviposition

Chapter Summary

Ovipositing insects need to strike a balance between laying eggs only on hosts that are optimal for offspring development and also accepting less favorable ones. On the one hand, high-quality hosts may be rare and search-times between oviposition events long; on the other hand, laying eggs on lower-quality hosts may lead to decreased larval performance. Every oviposition event thus carries opportunity costs mediated by time—since the time used to find a rare but high-quality host could have been used to find several more common but lower-quality hosts—and opportunity costs mediated by eggs—since eggs placed on low-quality hosts would have produced higher fitness returns on higher-quality hosts. A previous study aimed to use these time and egg costs to make inferences on the importance of egg and time limitation for strategic oviposition, claiming a large influence of egg limitation due to egg costs being higher than suggested by the mere incidence of egg limitation. In order to reexamine this conclusion, I expand the analytical oviposition model of the previous chapter where egg and time limitation are endogenous and not pre-supposed. The results show that including search times into the time costs of oviposition—as had not been done by the previous approach—lets the time and egg costs of oviposition become equal to the likelihoods of time and egg limitation, without a disproportionately high contribution of egg costs. A reanalysis of oviposition data from twelve insect species confirms that the previous model's estimations of time costs are greatly affected by the average search times between successful ovipositions. Despite these previous inaccuracies, however, the question remains how helpful such time and egg costs are to understanding strategic insect oviposition. In fact, partitioning the fitness derivative into changes proportional to the likelihoods of egg and time limitation, respectively, shows that schematic considerations of egg and time costs may be an oversimplification relative to the actual fitness costs of different oviposition strategies. As a result, evolutionary approaches as presented in the previous chapter may present a more insightful approach.

3.1 Introduction

Most research on insect oviposition has been dominated by approaches that considered either only the time cost or only the egg cost of oviposition because they assumed individuals to always be either time- or egg-limited in their oviposition (e.g. [15, 68]; summarized in [97]). In short, time-limited individuals die before laying their full egg complement while egg-limited individuals exhaust their full egg complement before dying (refer back to figure 1.1 on page 3 of chapter 1). Time and egg costs are thus two dimensions of the opportunity cost that is associated with oviposition: Time costs refer to the fact that time spent during oviposition cannot be used to perform other oviposition tasks, while egg costs refer to the fact

that an egg laid during oviposition now cannot be laid elsewhere later. Every oviposition event thus carries opportunity costs mediated by time and mediated by eggs [94]. These costs shape optimal oviposition strategies.

Time costs only have an effect on reproductive success if an individual becomes time-limited, egg costs only if it becomes egg-limited. As a result, differences in approach that stress either egg or time limitation carry far-reaching implications: If one is only time-limited, then egg costs are irrelevant and rate-maximization is the optimal oviposition strategy; if one is purely egg-limited, then time costs do not matter and one should only lay eggs on the best hosts regarding offspring performance, no matter how rare. In other words, oviposit everywhere (i.e., total generalism) if you possess an infinite number of eggs and oviposit ultra-selectively (i.e., complete specialism) if you are immortal. Since insects neither are immortal nor carry an infinite number of eggs, however, both egg and time costs contribute to oviposition costs and jointly shape oviposition strategies. Assessing the influence of these costs may therefore present a helpful approach to analyzing insect oviposition strategies [93, 103].

Historically, time limitation began as the dominating assumption (starting from [68]). Later, the frequently observed absence of preference-performance correlations—the fact that insects were found not to prefer those hosts for oviposition where their larvae performed best—lead to the incorporation of egg limitation into modeling theory (e.g., [15]). In the following, different schools of research emerged that, im- or explicitly, mostly focused either on only egg or on only time limitation in determining oviposition behavior (summarized in [97]). The debate on whether time or egg limitation is more important remains unresolved (compare [93] and [103]). As chapter 2 has demonstrated, neither phenomenon can safely be ignored in studies of strategic insect oviposition.

In this chapter, I reevaluate the contributions of time and egg costs to the total cost of oviposition. In contrast to previous approaches, I include the time spent searching for hosts into the cost of oviposition. Since the host searches preceding every oviposition event usually take much more time than the actual egg-laying [94], search times are an important component of insect time budgets. My results demonstrate that, as intuitively expected but contrary to previous results, the opportunity costs of oviposition mediated by time and by eggs are, respectively, equal to the likelihoods of becoming time- or egg-limited. Simply put, if one runs out of eggs during one's lifetime, then the current oviposition costs exactly one egg and time costs are irrelevant, but if one runs out of time, then the current oviposition costs exactly the time to lay one egg and egg costs are irrelevant.

Egg and time limitation, however, are not independent inputs to an insect's oviposition behavior but outputs of its oviposition strategy (see chapter 2). As a result, I sought to assess the validity of schematic egg and time costs in comparison to the actual fitness costs and benefits of different oviposition strategies. The results, which I derive from partitioning the fitness derivative into terms proportional to egg and to time limitation, highlight that such cost considerations may be overly simplistic. As a result, the evolutionary approach presented in the previous chapter may be more suitable to understanding the incidence of egg and time limitation in the wild and their contribution to strategic insect oviposition.

3.2 Model

A conceptual model to partition the oviposition costs of parasitoids into costs mediated by eggs and by time has been proposed by Jay Rosenheim [94]. I extend this model to phy-

tophagous insects by slightly modifying its wording with the term "hosts" referring to plant hosts of phytophagous larvae as well as insect hosts of parasitoids. This schematic model can be summarized as follows, with the text inside each pair of parentheses corresponding to the mathematical terms below it.

$$
\begin{array}{ccccc}
 & & & & \text{Cost of oviposition} = \\
\left(\begin{array}{c}\text{Number of hosts that}\\ \text{cannot be oviposited}\\ \text{on because of the}\\ \text{egg used, assuming}\\ \text{egg limitation}\end{array}\right) & \cdot & \left(\begin{array}{c}\text{Fitness return}\\ \text{per oviposition}\end{array}\right) & \cdot & \left(\begin{array}{c}\text{Probability of}\\ \text{egg limitation}\end{array}\right) \\
1 & \cdot & \Delta W & \cdot & P_{\text{egg-lim}} \\
+\left(\begin{array}{c}\text{Number of hosts that}\\ \text{cannot be oviposited}\\ \text{on because of the}\\ \text{time used, assuming}\\ \text{time limitation}\end{array}\right) & \cdot & \left(\begin{array}{c}\text{Fitness return}\\ \text{per oviposition}\end{array}\right) & \cdot & \left(\begin{array}{c}\text{Probability of}\\ \text{time limitation}\end{array}\right) \\
+\left((T_{\text{ovip}} - T_{\text{rej}}) \cdot r_{\text{ovip}}\right) & \cdot & \Delta W & \cdot & P_{\text{time-lim}}
\end{array}
$$

Here, ΔW is the fitness return per successful oviposition on a host, $P_{\text{egg-lim}}$ and $P_{\text{time-lim}}$ are the respective probabilities of egg and time limitation, T_{ovip} and T_{rej} are the respective times it takes to oviposit on or reject a host, and r_{ovip} is the rate of oviposition.

In order to examine this schematic approach to the egg and time costs of oviposition in more detail, I use the analytical model developed in the previous chapter. In this model for oviposition in proovigenic insects, females lay one egg per time period, survive to another period with probability q, and carry n eggs. A female thus becomes egg-limited with probability q^n and time-limited with complement probability $1 - q^n$. This approach presupposes neither egg nor time limitation. As derived previously (equations 2.1–2.4), this model gives for the number of eggs laid by a given female:

$$\mathrm{E}(Y) = \frac{q(1 - q^n)}{1 - q} \tag{3.1}$$

As elaborated in chapter 2, the probability q to survive to lay another egg is the complement of the probability of dying before another egg is laid, which is equal to the mortality rate divided by the sum of oviposition and mortality rate (see equation 2.5). In turn, the mortality rate μ can be assumed as constant if mortality is random and uncorrelated with oviposition.

I extend this model slightly by deriving average oviposition rates from the abundances of more than one suitable host species and from these host species' acceptance rates by ovipositing insects. I take m suitable host species to be present, each with an abundance f_i and an acceptance rate a_i. Encounter rates with a given host plant species are assumed to be equal to that species' abundance. Acceptance rates upon host encounter range from always accepted ($\mathrm{a}_i = 1$) to never accepted ($\mathrm{a}_i = 0$). Since host encounters are random, average oviposition rates can be calculated as the sum over all host abundances weighted by their respective acceptance rates (or, perhaps more intuitively, as the product of average acceptance rate $\overline{\mathrm{a}}$ and the abundance of all suitable hosts hosts $\sum_{i=1}^{m} \mathrm{f}_i$). This gives for the

probability to survive to lay another egg:

$$q = 1 - \frac{\mu}{\mu + \sum_{i=1}^{m} \mathrm{a}_i \mathrm{f}_i} = \frac{\sum_{i=1}^{m} \mathrm{a}_i \mathrm{f}_i}{\mu + \sum_{i=1}^{m} \mathrm{a}_i \mathrm{f}_i} \tag{3.2}$$

3.3 Results

3.3.1 Time and egg costs of oviposition

In order to include the time cost of searching into the cost of oviposition, I re-frame Rosenheim's approach in the context of my extended analytical model. Assuming host encounter to be random lets the rate of oviposition be the product of average acceptance rate $\overline{a}$ and abundance of all suitable hosts $\sum_{i=1}^{m} f_i$ (see above). Since the probability of egg limitation is the chance of surviving until all eggs are laid, I can represent it as $P_{\text{egg-lim}} = P(Y \geq n) = q^n$ (with Y as the number of eggs laid). Conversely, the probability of time limitation—the complement chance of dying before all eggs are laid—is $P_{\text{time-lim}} = P(Y < n) = 1 - q^n$. With the fitness return per oviposition set to $\Delta W = 1$ for simplicity, this gives for the weighted contribution of time costs to total cost of oviposition:

$$\begin{array}{rcccccccc} \text{Time cost} & = & T_{\text{ovip}}^{\text{tot}} \cdot r_{\text{ovip}} & \cdot & \Delta W & \cdot & P_{\text{time-lim}} & & \\ & = & \frac{1}{\overline{a} \sum_{i=1}^{m} f_i} \cdot \overline{a} \sum_{i=1}^{m} f_i & \cdot & 1 & \cdot & (1 - q^n) & = 1 - q^n \end{array} \tag{3.3}$$

Here, the oviposition time $T_{\text{ovip}}^{\text{tot}}$ (i.e., the reciprocal of the rate of oviposition, r_{ovip}) represents the *total* time required for one successful oviposition and thus does not include an explicit rejection time T_{rej}.

Analogously, I calculate the weighted contribution of egg costs to total cost of oviposition as:

$$\begin{array}{rcccccccc} \text{Egg cost} & = & 1 & \cdot & \Delta W & \cdot & P_{\text{egg-lim}} & & \\ & = & 1 & \cdot & 1 & \cdot & q^n & = q^n \end{array} \tag{3.4}$$

Taken together, these results present a simple but illustrative picture of the contributions of time and egg costs to the total cost of oviposition. As before, the number of hosts that cannot be oviposited on *because of the egg used* is always one—one egg laid here cannot be laid elsewhere (see equation 3.4). However, the number of hosts that cannot be oviposited on *because of the time used* now also is one—in the time used to lay this egg, exactly one other egg could have been laid elsewhere (see equation 3.3). As a result, the oviposition cost mediated by time is the probability of time limitation, and the cost mediated by eggs is the probability of egg limitation, which together add up to one:

$$\text{Cost of oviposition} = q^n + (1 - q^n) = 1 \tag{3.5}$$

In summary, one oviposition costs on average exactly the time that were needed for laying another egg and exactly one egg. That is, there is an opportunity cost of one egg if time limitation occurs and an opportunity cost of one egg if egg limitation occurs. Since animals always become either egg or time-limited, the expected cost of oviposition adds up to unity. The simplicity of these findings may call into question the usefulness of time and egg costs to analyze strategic oviposition behavior (see below). Nevertheless, these results suggest that, in contrast to previous findings [94], egg limitation does not have disproportionate effects beyond its incidence levels on the opportunity costs of oviposition.

3.3.2 The marginal costs and benefits of oviposition strategies

As described above, the opportunity costs of oviposition have previously been compartmentalized into costs mediated by eggs and by time [94]. In essence, the presented argument was that because costs mediated by eggs exceed those mediated by time, egg limitation plays a more important role for optimal oviposition than its incidence would suggest. From an evolutionary point of view, however, it seems more sensible to derive the marginal costs and benefits of different oviposition strategies directly from the fitness function. As we will see, however, the resulting costs and benefits are less straightforward than the previously suggested egg and time costs of oviposition.

I derive the marginal fitness costs and benefits of increasing the number of eggs at eclosion by differentiating the fitness function derived in the previous chapter (eq. 2.7) with respect to the number of eggs at eclosion, n. I begin by writing the fitness-function as conceptualized in equation 2.8 with $R_{\max}$ denoting an insect's maximal rate of reproduction (i.e., oviposition rate f over mortality rate μ) and $P_{\text{time-lim}}$ and $P_{\text{egg-lim}}$ the risks of time and egg limitation. Since, as before, the insect's mortality rate μ is a monotonically increasing function of egg number n—the exact trade-off shape needs not be specified here—the terms $R_{\max}$ and $P_{\text{time-lim}}$ also become functions of n.

$$w(n) = \frac{f}{\mu(n)} \cdot \left(1 - \left(\frac{f}{f+\mu(n)}\right)^n\right) = R_{\max}(n) \cdot P_{\text{time-lim}}(n)$$

Differentiating this fitness function by use of the product rule makes clear that the fitness costs and benefits of increasing one's egg complement consist of two terms, one of which is proportional to the risk of time limitation.

$$\frac{dw}{dn} = \frac{dR_{\max}}{dn} \cdot P_{\text{time-lim}} + \frac{dP_{\text{time-lim}}}{dn} \cdot R_{\max} \tag{3.6}$$

It is easier to compute these two derivatives with respect to n separately. When replacing $P_{\text{time-lim}}$ and $R_{\max}$ with the more complex terms from equation 3.3.2, this gives:

$$\begin{aligned} \frac{dR_{\max}}{dn} &= \frac{d}{dn}\left(\frac{f}{\mu(n)}\right) = -\frac{f}{(\mu(n))^2} \cdot \frac{d\mu}{dn} \\ \frac{dP_{\text{time-lim}}}{dn} &= \frac{d}{dn}(1 - P_{\text{egg-lim}}) = -\frac{d}{dn}(P_{\text{egg-lim}}) \end{aligned} \tag{3.7}$$

The lower term can be differentiated by taking the logarithm of the equation for $P_{\text{egg-lim}}$ and differentiating the resulting term on both sides with respect to n while keeping in mind the product and chain rule of differentiation. This results in:

$$\begin{aligned} P_{\text{egg-lim}} &= \left(\frac{f}{f+\mu(n)}\right)^n \\ \Leftrightarrow \ln(P_{\text{egg-lim}}) &= n \cdot \ln\left(\tfrac{f}{f+\mu(n)}\right) \\ \Leftrightarrow \tfrac{1}{P_{\text{egg-lim}}}\tfrac{dP_{\text{egg-lim}}}{dn} &= \tfrac{d}{dn}\left(n \cdot \ln\left(\tfrac{f}{f+\mu(n)}\right)\right) \\ \Leftrightarrow \tfrac{dP_{\text{egg-lim}}}{dn} &= P_{\text{egg-lim}} \cdot \left(\ln\left(\tfrac{f}{f+\mu(n)}\right) + n \cdot \tfrac{d}{dn}\left(\ln\left(\tfrac{f}{f+\mu(n)}\right)\right)\right) \\ \Leftrightarrow \frac{dP_{\text{egg-lim}}}{dn} &= P_{\text{egg-lim}} \cdot \left(\ln\left(\frac{f}{f+\mu(n)}\right) - \frac{n}{f+\mu(n)} \cdot \frac{d\mu}{dn}\right) \end{aligned} \tag{3.8}$$

Finally, I can reenter the results from equations 3.7 and 3.8 into equation 3.6, which gives:

$$\begin{aligned}\frac{dw}{dn} = & -\frac{f}{(\mu(n))^2}\cdot\frac{d\mu}{dn}\cdot P_{\text{time-lim}} \\ & -\frac{f}{\mu(n))}\cdot P_{\text{egg-lim}}\cdot\left(\ln\left(\frac{f}{f+\mu(n)}\right)-\frac{n}{f+\mu(n)}\cdot\frac{d\mu}{dn}\right)\end{aligned}$$

In order to interpret this complex formula biologically, I replace $f/f+\mu(n)$ with the probability to live to lay another egg q as well as $f/\mu(n)$ with $R_{\max}$, while changing the order of terms slightly. This results in the following formula for the marginal costs and benefits of increasing one's egg complement:

$$\frac{dw}{dn} = R_{\max} P_{\text{egg-lim}}\left(\frac{n}{f+\mu(n)}\frac{d\mu}{dn}-\ln q\right)-\frac{1}{\mu(n)} R_{\max} P_{\text{time-lim}}\frac{d\mu}{dn} \tag{3.9}$$

I can use equation 3.6 to see that the first term in the sum of equation 3.9 represents the marginal benefit of increasing the number of eggs as mediated by the resulting increased risk of time limitation while the second term represents the marginal cost of increasing the number of eggs as mediated by the resulting decreased maximum reproductive potential. At the evolutionary optimum, these two terms cancel out exactly.

Three findings from the biological interpretation of these marginal costs and benefits come as no surprise: (1) Marginal costs scale with the risk of time limitation and marginal benefits with the risk of egg limitation—the benefits of having more eggs are higher if egg limitation is common, but the costs are higher if time limitation is common. (2) Reproductive potential affects marginal costs and benefits equally and its value (but not how it changes with n) is thus irrelevant for the evolutionarily stable number of eggs. (3) Both marginal costs and benefits are affected by how mortality changes with increasing egg number.

Other findings are less easily explained. Mortality, for instance, affects marginal costs and benefits in the same direction but not the same manner. Moreover, the marginal benefits of increasing egg load scale with a hardly interpretable term that includes the logarithm of the probability to live to lay another egg and that arises from the mathematical structure of the likelihood of egg limitation (see eq. 3.8).

Comparing these marginal fitness costs and benefits to the previously suggested opportunity costs of oviposition [94] shows some similarities—that one component scales with the risk of time, the other with the risk of egg limitation—but confirms the intuition that these schematic costs may be too straightforward to capture the actual costs and benefits of different oviposition strategies. However, this finding does not speak against the evolutionary significance of egg limitation for optimal oviposition strategies. It is just that, with the correct cost argument being so complicated, the evolutionary *importance* of egg limitation in optimal oviposition may be shown more clearly and more intuitively by the fitness-underestimation of ignoring egg limitation (refer back to figure 2.5 on page 13 of chapter 2). At the same time, the evolutionary *emergence* of egg and time limitation may be more appropriate examined using such trade-off based modeling approaches as are presented in chapter 2.

3.4 Discussion

Ovipositing insects can be limited in their egg-laying strategies both by the time available and by the number of eggs they carry. I have used a simple model to reevaluate how these two factors, time and eggs, contribute to the cost of oviposition. My results show that the

relative contributions of time and eggs are proportional to the probabilities of time and egg limitation. Thus, neither egg nor time costs play negligible roles in shaping insect oviposition. However, since egg limitation has been found to occur far less often than time limitation, my findings suggests a strong role for ecological factors like host distribution that determine the likelihood of time limitation. Additionally, a comparison of schematic time and egg costs with the actual fitness costs and benefits of increasing one's egg load suggests that more extended evolutionary models as presented in the previous chapter may be more productive for the analysis of strategic insect oviposition.

3.4.1 The importance of search times

The defining feature of my model is that I include the time spent searching for hosts into the cost of oviposition. This remedies the apparent paradox that the relative contribution of oviposition costs mediated by time *decreases* with increasing search times because, as long as one excludes search times, the opportunity cost of the time spent to lay an egg shrinks with decreasing oviposition rates. As a result, the contributions of time to the cost of oviposition as estimated by my approach grow markedly relative to previous results, where estimates of the contribution of egg costs to oviposition costs based on empirical data often exceeded 50% despite low probabilities of egg limitation of around 10% [94].

Reevaluating these data demonstrates differences in the proportions of egg and time costs to arise mostly due to differences in the product of net oviposition time (i.e. the difference between the time to oviposit on and to reject a host, $T_{\text{ovip}} - T_{\text{rej}}$) and oviposition rate, r_{ovip} (Figure 3.1a, compare table 3.1). Moreover, excluding search times from oviposition costs produces the counter-intuitive result that large contributions of time costs occur for short search times and small contributions for long search times (Figure 3.1b). This is because intervals between oviposition events are usually an order of magnitude larger than the time needed for a single oviposition (Table 3.1).

Table 3.1. Summary of oviposition data from ([94], first 12 lines) and ([97], last line). All times are given in seconds and rates in eggs per hour. Search times calculated as reciprocal of oviposition rate, egg and time costs calculated as in equation 3.3.

Taxon	T_{rej}	T_{ovip}	r_{ovip}	$\frac{T_{\text{ovip}}-T_{\text{rej}}}{1/r_{\text{ovip}}}$	$P_{\text{egg lim}}$	Egg cost	Time cost
Aphytis aonidae	294	570	0.4	0.031	0.09	76%	24%
Aphytis vandenboschi	1056	1236	0.43	0.022	0.09	82%	18%
Comperiella bifasciata	55	203	2.04	0.084	0.09	54%	46%
Anicetus beneficus	-	318	2.1	0.186	0.09	35%	65%
Asobara tabida	4	29.8	1.78	0.013	0.07	86%	14%
Leptopilina heterotoma	4	29.2	2.89	0.020	0.09	83%	17%
Leptopilina clavipes	1.8	40	0.88	0.009	0.13	94%	6%
Aphaereta minuta	-	22.5	2.31	0.014	0.09	87%	13%
Pauesia unilachni	59	234	2	0.097	0.09	50%	50%
Lysiphlebus cardui (+ ants)	19	57	21.6	0.228	0.09	30%	70%
L. cardui (without ants)	19	57	13.3	0.140	0.09	41%	59%
Aphidius rosae	-	1.5	5.8	0.002	0.09	98%	2%
Rhopalomyia californica	-	10	58	0.16	0.17	57%	43%

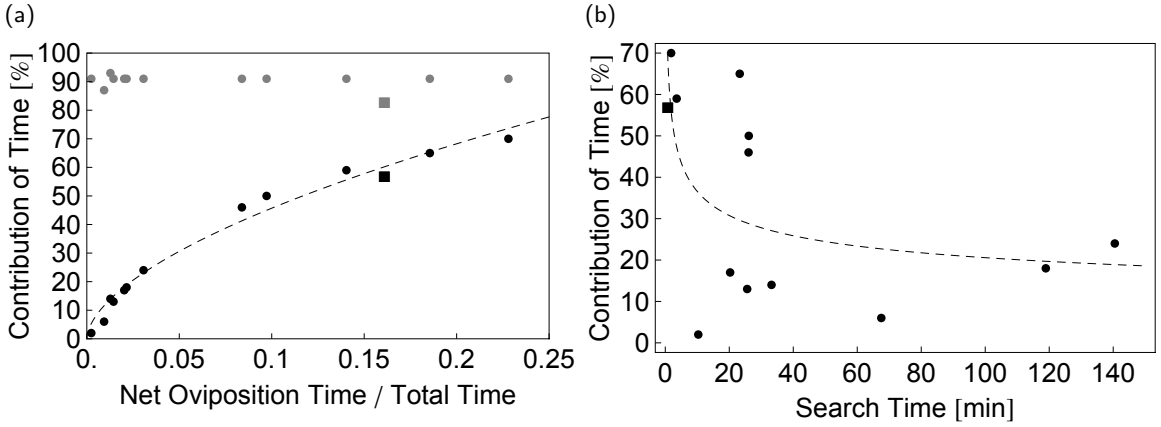


Figure 3.1. Reanalysis of the contribution of time costs to the total cost of oviposition in 11 parasitoid and 1 phytophagous insect species (circles, data from [94]; square, data from [97]). In panel A, the ratio of net oviposition time, the difference between time needed to accept and to reject a host, and total time is considered ($^{T_{\text{ovip}}-T_{\text{rej}}}/_{1/r_{\text{ovip}}}$); shown in gray are my estimates of time-contributions, which correspond to the probability of time limitation. In panel B, only search times ($^{1}/_{r_{\text{ovip}}} - T_{\text{ovip}}$) are considered. Note that, according to previous analyses [94], time costs rise with increasing oviposition time relative to total time (panel A) and sink, paradoxically, with increasing search times between oviposition events (panel B). All data as shown in table 3.1. Black dashed lines are significant non-linear regression lines with $y = c \cdot x^d$ (Panel A: $c = 173.1$, $P_c \approx 10^{-8}$, $d = 0.58$, $P_d \approx 10^{-9}$; Panel B: $c = 65.0$, $P_c \approx 10^{-3}$, $d = -0.25$, $P_d \approx 0.03$).

Including the time spent searching for hosts into the cost of oviposition does not imply that insects should oviposit on a specific host just because they already invested time into searching for it—such reasoning would indeed resemble Dawkins and Carlisle's "concord-fallacy" [18, 94]. Instead, rejecting one host leads to a *new* search before another oviposition opportunity arises because *every* oviposition decision is preceded by a host search. As a result, the time spent searching for hosts must be included into the time cost of optimal oviposition.

Following this intuition and including search times into the cost of oviposition decreases the relative influence of egg limitation on optimal oviposition strategies relative to previous approaches (see figure 3.1a). Whether individuals pursue rate- or quality-maximizing strategies now depends only on the probabilities of egg and time limitation (see equation 3.5). Since time limitation is found to occur with higher probability than egg limitation [52, 94], my finding thus suggest that time-mediated costs should have large effects on insect oviposition strategies.

3.4.2 The relative roles of egg and time limitation

Still, egg limitation is not a negligible factor, and costs mediated by eggs also contribute to oviposition costs. Egg limitation has been shown to occur in natural populations and may be explained by life-history selection pressures that penalize over-sized egg complements which, in combination with environmental stochasticity, makes it unlikely for individuals to always

match egg number with oviposition opportunity [94, 97]. However, because egg limitation is a minority condition, the results presented here suggest that its effects on oviposition strategies are correspondingly small, but far from insignificant (see chapter 2). Ecologically, for instance, thought experiments can be constructed where, though most females are time-limited, all eggs are laid by the few egg-limited females [95].

On evolutionary terms, the occurrence of egg and time limitation determines the fitness consequences of different oviposition strategies. While time limitation implies a fecundity penalty associated with rejecting poor-quality hosts (i.e. "don't waste time"), egg limitation conversely implies a fecundity penalty associated with accepting such hosts (i.e. "don't waste eggs"—[89]). In other words, ovipositing on a poor-quality host only carries opportunity costs if the egg could have been placed on a higher-quality host, whereas not ovipositing on said host only carries costs if the "wasted" search time reduces lifetime reproductive success. Additionally, strategic oviposition decisions feed back on the probability of becoming egg- and time-limited: Accepting a host and laying an egg decreases the perceived risk of time and increases that of egg limitation, whereas rejecting a host does just the opposite (refer back to figure 1.2 on page 4 of chapter 1). This dynamic nature of oviposition decisions is reproduced by the many dynamic programming approaches to optimal egg-laying behavior (e.g. [12]). The static approach put forward in this chapter, however, represents a more tractable way to examine how opportunity costs mediated by time and eggs influence the evolution of ovipositing strategies that maximize lifetime reproductive success.

How likely egg and time limitation are to occur in specific systems is determined by developmental and ecological factors. Generally, ecological factors such as host abundance will have a larger influence on time limitation since they determine encounter rates of acceptable hosts and, therefore, average search times. Conversely, developmental factors such as egg number (in proovigenic species) or egg maturation rates (in synovigenic species) have a larger effect on the probability of egg limitation because, simply put, individuals with few eggs or slow egg maturation are more likely to run out of eggs. As a result, the increased contributions of time-mediated costs that are revealed by my analysis suggest a stronger role for ecological factors in shaping optimal oviposition strategies. Additionally, time and egg limitation may interact to shape the co-evolution of relevant physiological traits and ecological factors. For instance, egg load and host density correlate positively in a proovigenic parasitoid [56], whereas lifespan and diet breadth correlate negatively in female Lepidoptera [56]. Moreover, as discussed briefly in the previous chapter, female *Leptidea sinapis* butterflies have been shown to differentially allocate resources to reproduction depending on their own body size as well as host plant availability [5].

3.4.3 Conclusion

In summary, my reassessment of time and egg costs suggests that, while both egg and time limitation make non-negligible contributions to the cost of oviposition, time limitation is likely to be the dominating factor in shaping optimal oviposition strategies. Since time limitation is tightly connected to host distribution patterns, my findings strengthen the idea that the absence of preference-performance correlations may be due to optimal hosts being rare [113]. In line with such predictions on the effects of host abundance, Lepidoptera species that oviposit on abundant hosts have indeed been found to have smaller diet breadths than species who lay eggs on rare hosts [52, 56]. As a result, the increased role of host distribution patterns in shaping optimal oviposition strategies provides an additional explanation for the puzzling, seemingly maladaptive egg-laying strategies of some insects: If good hosts are too

rare, it just may not pay to search for them.

At the same time, partitioning the fitness derivative into costs mediated by time and by eggs calls into question the validity of schematic time and egg costs for an evolutionary analysis of strategic insect oviposition. Egg and time limitation are very helpful concepts when examining the fitness consequences of different oviposition behaviors because they affect the fitness consequences of oviposition decisions, favoring anything from pure rate maximization to pure quality maximization (see above and chapter 1). Time and egg costs, however, may be less helpful tools for evolutionary analysis. This is because, as this chapter shows, while schematic cost considerations may be intuitively appealing, the actual fitness costs and benefits are less easily interpreted. Even the schematic approaches, however, do not support such a disproportionately large role for egg limitation in affecting strategic oviposition as had been advocated previously [94].

Taken together, this and the previous chapter demonstrate how insect oviposition strategies are the result of both ecological and evolutionary processes. On the one hand, as was the focus of chapter 2, evolutionarily stable egg-loads and risks of egg and time limitation result from the allocation of resources constrained by the well-known trade-off between survival and reproduction and, quantitatively, depend critically on the details of this trade-off. On the other hand, as this chapter demonstrates, a given level of egg and time limitation will determine the opportunity costs associated with oviposition on ecological time scales. However, my reassessment of previous schematic approaches to the time and egg costs of oviposition shows that trade-off based approaches as advocated in chapter 2 may prove more valuable when assessing the evolutionary emergence and importance of egg and time limitation in the context of strategic insect oviposition.

4 The evolution of generalism in heterogeneous environments

Chapter summary

How ecological niches change over evolutionary time is a long standing question in ecology. In insects, phylogenetic data suggest that the evolution of niche breadths—here the number of host species upon which an insect lays its eggs—entails the recurrent emergence of generalism from specialism. In this context, spatial heterogeneity has been identified as a central factor promoting the evolution of generalism. At the population dynamic level, however, differences in productivity within heterogeneuous habitats are likely to lead to emergent source sink dynamics that influence evolutionary dynamics. Here, I derive a straightforward optimization model of insect oviposition and contrast this model with its population genetic implementation in a spatially explicit source-sink context. This approach demonstrates the importance of gene flow and population structure in the question of how environmental heterogeneity may favor generalism over specialism. Specifically, I show spatial heterogeneity to be a necessary but not a sufficient condition for the evolution of generalism. Whereas the optimality model demonstrates that specialist strategies are favored in homogeneous environments but generalist strategies in heterogeneous ones, the spatially explicit population genetic implementation of this model shows how emergent source-sink dynamics may impede the spread of generalist strategies. Instead, specialism remains the evolutionarily stable strategy unless performance differences between patches are small or migration rates large, and I use an invasion fitness approach to derive analytically the threshold migration rates below which a generalist mutation does not spread. My results demonstrate the importance of eco-evolutionary approaches when studying patterns of host association in phytophagous insects.

4.1 Introduction

The relationship between phytophagous insects and their host plants is one of the core subjects of evolutionary biology [26]. A central feature of this relationship is an insect's diet breadth—the number of plant species that this species feeds upon as larvae and adults. Changes in a species' diet breadth may have far reaching ecological and evolutionary consequences. Host preferences may influence insect dispersal patterns and habitat colonization rates [40]; diet breadth may determine the impact of invasive plant species on generalist and specialist consumers [11]; and the formation of host races with diverging diet breadths may facilitate sympatric speciation [23].

An insect species' diet breadth is hardly stable on evolutionary time scales [112]. While it is difficult to evaluate in individual cases how and why the number of used host species changes, the question of how wide a diet breadth should be—whether individuals should be generalists or specialists—has received much attention [44, 68, 112, 125]. Generally,

species are expected to be specialists if resources are constant or abundant and generalists if resources are inconstant, unstable, or rare [31, 32, 63].

Among phytophagous insects, however, generalist species whose larvae perform well on a large number of different hosts seem to be rare, possibly due to the constraints and costs of coping with different host plants [60, 84, 116]. Instead, most species specialize on only few host plants, and phylogenetic analyses can help reconstruct the evolutionary dynamics of these host-plant specializations [53]. A detailed analysis on nymphalid butterflies shows that, while the ancestral species is likely to have been a specialist, increases in diet breadth must have occurred repeatedly during the many host shifts detected on evolutionary time scales [55]. This is because host switches entail oscillations in diet breadth from specialism on ancestral host, to generalism on ancestral and novel host, and back to specialism on the novel host [54]. As a result, according to this "oscillation hypothesis", the evolution of generalism from specialism plays a central role in generating the global diversity of plant-feeding insects.

Spatial heterogeneity is an important factor in such niche expansions and thus in the evolution of generalism from specialism [32, 63, 113, 116]. Specifically, increasing spatial variation in host plant abundance can result in generalists outperforming specialists in patches where the specialists' preferred host is rare or absent. As a result, generalist strategies with larger diet breadths may be under positive selection as individuals adapt to spatially varying local conditions. The resulting patterns of generalism and specialism emerge from a combination of gene flow between and reproduction within habitat patches [81].

When reproductive success varies between patches, however, the fact that migrant flow tends to be higher from densely populated to sparsely populated areas will lead to the emergence of source-sink dynamics [22, 62, 67, 88]. The resulting asymmetric gene flow is likely to influence the evolutionary dynamics of diet breadth expansions [1, 63]. Specifically, source-sink dynamics are likely to decrease the favorable effect of spatial heterogeneity on the evolution of generalism because there is little natural selection on performance in low productive sinks and because gene flow from ancestral sources—where specialism is optimal—may swamp local adaptation in sinks [62, 65]. On a more conceptual level, the phenomenon that insects tend to adapt to better-than-average conditions in sources but not to worse-than-average conditions in sinks falls within the theory of adaptive optimism and pessimism (see section 1.4 and [75]).

This chapter takes on two perspectives to examine the evolution of generalism from specialism when an insect species interacts with two hosts that differ in larval performance. First, I use an optimality model to assess whether generalist or specialist oviposition is advantageous in the presence or absence of spatial heterogeneity in host abundance. Then, I implement these reproductive strategies in a population genetic context to examine the effect of emergent source-sink dynamics on the evolution of generalism from specialism. I find that, while generalism is often advantageous in the simple optimality model, it usually does not spread in the population genetic model unless performance differences are small or migration rates large. I discuss these results with regard to the feedback between ecological and evolutionary dynamics that is induced by emergent source-sink dynamics and, more generally, with regard to the evolutionary relationships between phytophagous insects and their host plants.

4.2 Model

4.2.1 Optimal oviposition

For my analytical approach to the evolution of generalist strategies, I expand the model of chapter 2 (equations 2.1–2.4) to include several host species, differential host acceptance by insects, as well as differential larval performance in terms of offspring survival on the different host species. The model presupposes neither egg nor time limitation and calculates the number of eggs laid by a given proovigenic female as a function of that female's egg number at eclosion, n, and its survival rate until the next oviposition event, q. With the derivation as presented in chapter 2, the expected number of eggs Y laid by any female can be calculated as:

$$\mathrm{E}\left(Y\right) = \frac{q\left(1-q^{n}\right)}{1-q} \tag{4.1}$$

Next, I examine how ecological circumstances and individual oviposition strategies map onto the probability to survive to lay another egg q. As before, this probability is the complement of the probability of dying before another egg is laid, which can be calculated as the rate of mortality divided by the sum of the rates of oviposition and mortality.

I assume mortality to be random and uncorrelated with oviposition so that insects die at a constant mortality rate μ. As before, mortality rate depends on investment in egg number via the trade-off between survival and reproduction (see below).

Regarding host encounter rates, I take m suitable host species to be present, each with an abundance f_i and a relative frequency F_i where $\mathrm{F}_i = {}^{\mathrm{f}_i}/_{\sum_{j=1}^{m}\mathrm{f}_j}$. Encounter rates are assumed to be equal to these abundance values.

Each host species i is accepted by females with an acceptance rate a_i that ranges from always accept ($\mathrm{a}_i = 1$) to never accept upon encounter ($\mathrm{a}_i = 0$). Oviposition rates are calculated as the sum over all host abundances weighted by their respective acceptance rates (or, similarly, as the product of average acceptance rate $\overline{\mathrm{a}}$ and abundance of all suitable hosts hosts $\sum_{i=1}^{m}\mathrm{f}_i$).

Taken together, the probability q of surviving to the next oviposition event is:

$$q = 1 - \frac{\mu}{\mu + \sum_{i=1}^{m}\mathrm{a}_i\mathrm{f}_i} = \frac{\sum_{i=1}^{m}\mathrm{a}_i\mathrm{f}_i}{\mu + \sum_{i=1}^{m}\mathrm{a}_i\mathrm{f}_i} \tag{4.2}$$

I combine equations 4.1 and 4.2 to arrive at a formula that maps ecological circumstances and individual oviposition strategies onto reproductive output. That is, it calculates the number of oviposited eggs from the abundance of suitable hosts and the rates at which females accept these hosts upon encounter.

Finally, in order to integrate the cost of accepting sub-optimal hosts into female reproductive success, I consider how differential larval performance on different host species influences oviposition outcomes. I define larval performance p_i on host i as the percentage of eggs that survives until reproduction. Female reproductive success is calculated by multiplying the expected number of eggs with the average larval performance $\overline{\mathrm{p}}$, which is the sum over all performances p_i weighted by the proportion of eggs E_i laid on host i. With $\mathrm{E}_i = \frac{1}{\overline{\mathrm{a}}}\,\mathrm{a}_i\,\mathrm{F}_i$ this gives:

$$\overline{\mathrm{p}} = \sum_{i=1}^{m}\mathrm{p}_i\mathrm{E}_i = \frac{1}{\overline{\mathrm{a}}}\sum_{i=1}^{m}\mathrm{p}_i\mathrm{a}_i\mathrm{F}_i = \frac{\sum_{i=1}^{m}\mathrm{p}_i\mathrm{a}_i\mathrm{F}_i}{\sum_{i=1}^{m}\mathrm{a}_i\mathrm{F}_i} = \frac{\sum_{i=1}^{m}\mathrm{p}_i\mathrm{a}_i\mathrm{f}_i}{\sum_{i=1}^{m}\mathrm{a}_i\mathrm{f}_i} \tag{4.3}$$

I combine equations 4.1 to 4.3 to construct a coherent formula for female reproductive success. I can use this formula as a tool to determine optimal oviposition strategies in different ecological situations by numerically maximizing reproductive success as a function of acceptance rates a_i and size of egg complement n, as constrained by the life history trade-off between μ and n. All calculations were performed using Mathematica 7.0 (Wolfram Research, Inc.) and by hand.

4.2.2 Population genetic model

I implement different oviposition strategies in a population genetic context in order to assess the evolution of generalist oviposition strategies in heterogeneous environments. Since I am interested in how spatial heterogeneity may facilitate the evolution of generalism, I consider the fate of generalist mutants with wider diet breadths than their wildtype specialist conspecifics. I use a system of two patches connected by bidirectional migration as a spatial scenario that is general enough for my purposes but still allows for analytical approaches to its dynamics.

Individuals are haploid and reproduce asexually. I represent allele-frequencies in both patches by x_{ij} where subscript i determines patch number and subscript j represents phenotype (1 : wildtype, 2 : mutant). Population growth is density-dependent, the strength of which is regulated by parameter b. Reproductive success of mutants and wildtypes differs between patches with reproductive rates denoted by r_{ij} (subscripts as before). Reproductive rates will later be calculated from ecological circumstances and oviposition strategies using the optimality framework presented in equations 4.1 to 4.3. Migration takes place after eclosion but before reproduction, and migration rates are denoted by m_{ij} with subscripts indicating direction of gene flow. This approach gives for the recursion equations for both patches:

$$\begin{aligned} x'_{1j} =& r_{1j}\,\tilde{x}_{1j}\left(1 - b\sum_l \tilde{x}_{1l}\right) \\ & \text{with } \tilde{x}_{1j} = (1 - m_{12})\,x_{1j} + m_{21}x_{2j} \end{aligned} \tag{4.4}$$

$$\begin{aligned} x'_{2j} =& r_{2j}\,\tilde{x}_{2j}\left(1 - b\sum_l \tilde{x}_{2l}\right) \\ & \text{with } \tilde{x}_{2j} = (1 - m_{21})\,x_{2j} + m_{12}x_{1j} \end{aligned} \tag{4.5}$$

As before, analytical calculations were performed using Mathematica 7.0 (Wolfram Research, Inc.) and by hand. Numerical simulations were performed using C++ and the DevC++-compiler (Bloodshed Software).

4.3 Results

I examine whether spatial heterogeneity in host availability will lead to the emergence of generalist oviposition strategies. Specifically, I envision a scenario where a specialist colonizes a new patch or habitat with different host plant distribution, so that optimal oviposition strategies in the novel habitat differ from those in the ancestral patch. Will individuals adopt generalist strategies that give higher reproductive success in the novel patch at a cost

to reproduction in the ancestral patch? I approach this question from two sides, that of optimality modeling of oviposition strategies and that of the population genetics of these strategies.

4.3.1 Optimal oviposition

As long as larval performances do not differ between potential hosts, wider host ranges trivially lead to higher reproductive success (see equations 4.1 to 4.3). I therefore focus on cases with differential larval performance on the two hosts. For greater ease of analysis, I chose the simplest trade-off among the three shapes analyzed in chapter 2 and assumed a linear interdependence between size of egg complement and mortality rate without a baseline mortality (i.e., $n = c \cdot \mu$). In the analysis below, the scaling factor c was set to $c = 0.0001$. I then determine optimal oviposition strategies by numerically maximizing female reproductive success over both acceptance rates and size of egg complement.

Larval performance and the number of successfully laid eggs jointly determine reproductive success in my model. Therefore, I expect the emergence either of preference-performance correlations, where host quality positively correlates with host acceptance, or of generalist strategies where acceptance rates do not co-vary with host quality. Since generalism carries a cost in reduced larval performance and specialism carries a cost in the lower number of eggs that are laid, the number of oviposition events may potentially have a larger influence on reproductive success than larval performance, for example if high-quality hosts are rare or performance differences small.

In the absence of spatial heterogeneity, generalism is only adaptive for low performance differences, and preference-performance correlations emerge as soon as differences in host quality increase (figure 4.1, left panel). At intermediate performance differences, lower-quality hosts are only accepted if their proportion among suitable hosts is very large, with acceptance thresholds increasing with larger performance differences. For very large performance differences, lower-quality hosts are only accepted if they are the only host present, otherwise preference-performance correlations prevail (figure 4.1, left panel).

In order to introduce spatial heterogeneity, I assume the population to be structured into two patches: a “good” patch where both higher- and lower-quality hosts occur and a “bad” patch with only lower-quality hosts. I vary the proportion of lower-quality hosts in the “good” patch—that is the cost of adaptation that a generalist incurs in terms of reduced average larval performance—and then determine optimal oviposition strategies. To do so, I maximize average reproductive success in both patches instead of in a single patch since I am seeking a globally optimal strategy.

This approach yields generalism as the prevalent strategy across large parts of the parameter space. Spatial heterogeneity in host distribution leads to the disappearance of preference-performance correlations, likely because specialist reproduction fails completely in patches where preferred hosts are absent. Only when performance on the lower-quality host is very poor—here 0.5% survival to reproduction compared to 5% on the higher-quality host—and when the lower-quality hosts is reasonably abundant in the “good” patch is it ever optimal to adopt a specialist oviposition strategy (figure 4.1, right panel).

4.3.2 Population Genetic Model

The differential reproductive success of generalists and specialists in the two patches have consequences for demography and gene flow that are ignored by abstract optimality ap-

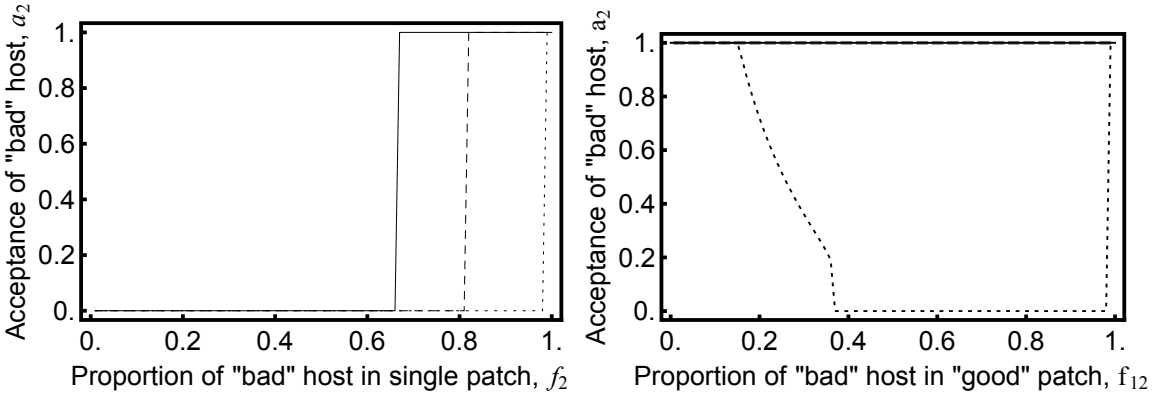


Figure 4.1. Optimal acceptance rates of lower-quality hosts in response to changes in host abundance. Acceptance rates of lower-quality host, a_2, in a single population (left panel) and in a two-patch metapopulation (right panel, for specifics see main text) as a function of the proportion of that host, f_2. Data are generated by numerically optimizing equations 4.1–4.3 over acceptance rates, a_i, and size of egg complement, n. Larval performance on higher-quality host is set to $p_1 = 5\%$. Performance on lower-quality host is varied between $p_2 = 1.5\%$ (solid line), $p_2 = 1\%$ (dashed line), and $p_2 = 0.5\%$ (dotted line). Total host abundance in each patch is kept constant at unity.

proaches. To study these effects, I use a population genetic model (equations 4.4-4.5) and examine a scenario with two patches and two hosts that differ in larval performance. I compare wildtype specialists that accept only the higher-quality host with mutant generalists that indifferently lay eggs on either host species. I take the higher-quality host to be common in one patch, here patch 1, but absent from the other, here patch 2, and the lower-quality host to be common in patch 2 but uncommon in patch 1. For easier reference, I call patch 1 the "good" and patch 2 the "bad" patch.

This spatial scenario leads to emergent source-sink dynamics where different habitat qualities lead to higher population densities in patch 1 than in patch 2 so that migration is stronger from patch 1 to patch 2 than vice versa. Wildtype specialist populations are self-sufficient only in patch 1 but not in patch 2, where they fail to reproduce. Mutant generalists reproduce successfully in both patches, though not at self-sufficient rates in patch 2, and always at lower rates than wildtypes in patch 1 because of decreased average larval performance. Patch 1 represents a source and patch 2 a sink if reproductive rates of all classes suffice the condition $r_{11} > r_{12} > r_{22}$ with $r_{21} = 0$.

Unfortunately, I was not able to solve the system of equations 4.4-4.5 analytically. Instead, I use an invasion fitness approach to approximate analytically the conditions where generalist strategies adapted to conditions in sink and source outcompete specialist strategies only adapted to conditions in the source. Additionally, I perform numerical simulations of the system of equations 4.4-4.5 to identify parameter values where only specialists, only generalists, or a polymorphism of both strategies persist.

For the invasion fitness approach, I use equation 4.4 to calculate the steady state of a

wildtype specialist in the absence of mutants:

$$x_{11}^{*} = \frac{r_{11}\left(1-m_{12}\right)-1}{b\, r_{11}\left(1-m_{12}\right)^{2}} \tag{4.6}$$

Without migration the population equilibrates at ${}^{r_{11}-1}/_{b\, r_{11}}$. I thus normalize population size to unity by setting the density-dependence parameter to $b = {}^{r_{11}-1}/_{r_{11}}$. Neglecting higher order terms and irrespective of choice of b, the population dynamics of an invading generalist are given by

$$x'_{12} = r_{12}\left(\left(1-m_{12}\right)x_{12} + m_{21}x_{22}\right)\left(\frac{1}{r_{11}\left(1-m_{12}\right)}\right) \tag{4.7}$$

$$x'_{22} = r_{22}\left(\left(1-m_{21}\right)x_{22} + m_{12}x_{12}\right)\left(1 - m_{12}\frac{r_{11}\left(1-m_{12}\right)-1}{r_{11}\left(1-m_{12}\right)^{2}}\right) \tag{4.8}$$

The generalist strategy spreads if the leading eigenvalue of the system rewritten in matrix form is larger than unity. As the matrix is non-negative with all real eigenvalues, the matrix' trace needs to be larger than two or the difference between trace and determinant less than one (since $\lambda_1 = {}^{\mathrm{Tr}}/_2 + \sqrt{{}^{\mathrm{Tr}^2}/_4 - \mathrm{D}}$, it holds that $\mathrm{Tr} > 2 \Rightarrow \lambda_1 > 1$ and that $\lambda_1 > 1 \Leftrightarrow \mathrm{Tr} - \mathrm{D} < 1$). For example, if the generalist also failed to have any offspring in the bad patch (i.e. $r_{22} = 0$), the determinant would be zero and the trace ${}^{r_{12}}/_{r_{11}}$. As a result, since specialist-fitness is higher than generalist-fitness in the good patch (i.e. $r_{11} > r_{12}$), generalist strategies are never adaptive if migration is absent.

Asymmetric critical migration rates

At low migration rates, the benefit of accepting the bad host in the bad patch and thus receiving some rather than no offspring does not balance the cost of accepting the bad host in the good patch. Increasing migration rates shifts this balance towards generalism, however, because it increases the selective relevance of performance in sinks.

I can show that a threshold migration rate exists above which a mutant generalist can invade for non-zero reproductive rates r_{11}, r_{12}, and r_{22}. I calculate this threshold migration rate by solving for the cases where either the matrix' trace becomes larger than two or the difference between trace and determinant smaller than one. For $r_{11} > r_{12} > r_{22}$, the first condition of $\mathrm{Tr} > 2$ always gives threshold migration rates greater than 0.5 and is therefore not biologically sensible. As a result, I solve the second condition of $\mathrm{Tr} - \mathrm{D} < 1$ to derive the critical migration rate from sink to source as a function of that from source to sink.

$$\begin{aligned} m_{21}^{\mathrm{crit}} = \; & \frac{\left(m_{12}-1\right)\left(r_{11}-r_{12}\right)}{\left(m_{12}+r_{11}-3m_{12}r_{11}+2m_{12}^{2}r_{11}\right)} \\ & \cdot\frac{\left(m_{12}r_{22}+r_{11}\left(m_{12}-1\right)\left(1-r_{22}+m_{12}\left(2r_{22}-1\right)\right)\right)}{\left(\left(m_{12}-1\right)r_{11}+r_{12}\right)r_{22}} \end{aligned} \tag{4.9}$$

Since generalism invades if $m_{21} > m_{21}^{\mathrm{crit}}$, the strength of migration in *both* directions jointly determines whether generalism may spread (figure 4.2). In fact, generalism may be adaptive both when relative migration rates are higher from the "good" to the "bad" patch as well as when the opposite is true (figure 4.2). Note that, as defined in the model (equations 4.4–4.5), migration rates are relative and not absolute—i.e., they determine the likelihood that

a given individual migrates to one patch from another. For instance, the *absolute number of migrants* from source to sink may be higher than vice versa even if *relative migration rates* are larger from sink to source.

As expected, threshold migration rates in either direction rise with increasing proportion of lower-quality hosts in patch 1 as well as with increasing differences in host quality. When differences in host quality or proportions of lower-quality hosts in patch 1 are large, however, generalism can never spread for biologically sensible migration rates (figure 4.2). As a result, individuals are likely to only adapt to conditions in the "good" source and not in the "bad" sink because gene flow from the highly productive source swamps local adaptation in the less productive sink, and because natural selection on performance in sinks is weak.

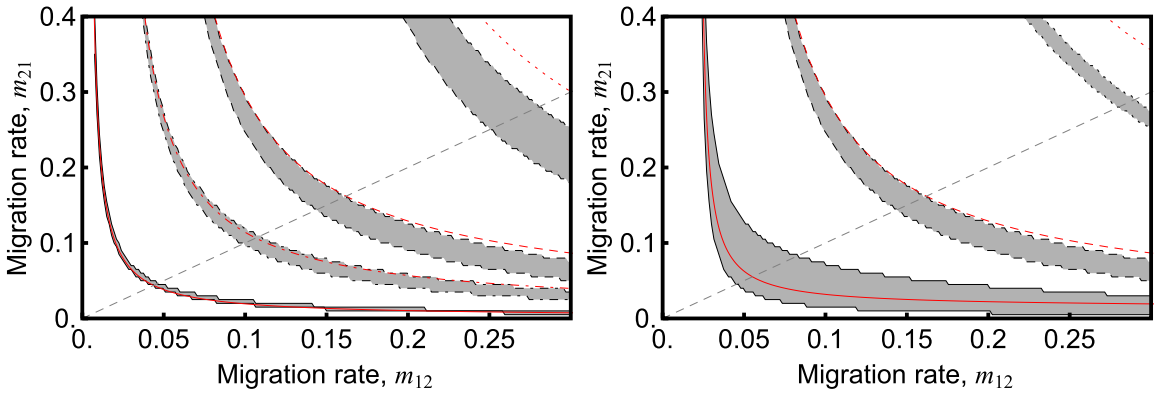


Figure 4.2. Threshold migration rates from sink to source, m_{21}^{crit}, for spread of generalist mutations in heterogeneous environments as functions of migration from source to sink, m_{12}. Generalist mutants do not spread below each lower black line and become fixed above each upper black line. In between each pair of black lines, areas of polymorphism between specialists and generalists are shaded in gray. Threshold migration rates were obtained through numerical simulation of equations 4.4–4.5 with reproductive rates r_{ij} calculated by maximizing the optimization model of equations 4.1–4.3. Each oviposition strategy was taken as present when its equilibrium frequency exceeded 0.1% and as fixed if it exceeded 99.9%. Red lines depict threshold migration rates as calculated by the analytical invasion fitness approach of equation 4.9. In the left panel, larval performance on the lower-quality host is set to $p_2 = 1\%$, while abundance of lower-quality hosts in patch 1 increases from lower left to upper right, i.e. $f_{12} = 0.01$ (solid lines), $f_{12} = 0.05$ (dash-dotted lines), $f_{12} = 0.1$ (dashed lines), to $f_{12} = 0.25$ (dotted lines). In the right panel, abundance of the lower-quality host is set to $f_{12} = 0.1$, while larval performance on the lower-quality host increases from lower left to upper right, i.e. $p_2 = 1.5\%$ (solid lines), $p_2 = 1\%$ (dashed lines), and $p_2 = 0.5\%$ (dotted lines). Other parameters are $f_{11} = 1 - f_{12}$, $f_{21} = 0$, $f_{22} = 1$, and $p_1 = 5\%$. The symmetric case of $m_{12} = m_{21}$ is illustrated by the dashed gray line, and symmetric critical migration rates are given by the intersect of the critical graphs with this line (see figure 4.3).

Symmetric critical migration rates

For the case of *symmetric* migration where asymmetries in gene flow only result from asymmetries in reproduction between the two habitat patches, I solve $m_{21}^{\text{crit}} = m_{12}$ to reveal four solutions. Two of these are complex conjugated, one is real and negative, and one is real and positive, the last of which constitutes the relevant critical symmetric migration rate m^{crit} above which generalist mutants will spread. As before, generalist mutants do not spread for biologically sensitive migration rates when difference in larval performance between lower and higher-quality hosts are large (figure 4.3).

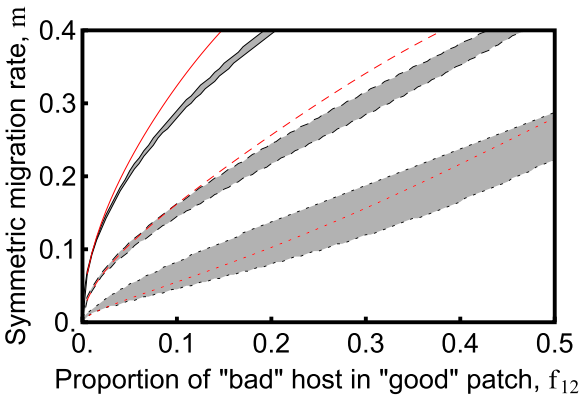


Figure 4.3. Threshold symmetric migration rates, m^{crit}, for spread of generalist mutations in heterogeneous environments as a function of the proportion of lower-quality hosts in the "good" source patch, f_{12}. Generalist mutants do not spread below each lower black line and become fixed above each upper black line. In between each pair of black lines, areas of polymorphism between specialists and generalists are shaded in gray. Threshold migration rates were obtained through numerical simulation of equations 4.4–4.5 with reproductive rates r_{ij} calculated by maximizing the optimization model of equations 4.1–4.3. Each oviposition strategy was taken as present when its equilibrium frequency exceeded 0.1% and as fixed if it exceeded 99.9%. Red lines depict threshold symmetric migration rates as derived from the analytical invasion fitness approach of equation 4.9. Larval performance on the lower-quality host is varied between $p_2 = 0.5\%$, $p_2 = 1\%$, and $p_2 = 1.5\%$ (solid, dashed, and dotted lines, respectively, increasing from upper left to lower right). Other parameters are $f_{11} = 1 - f_{12}$, $f_{21} = 0$, $f_{22} = 1$, and $p_1 = 5\%$.

Numerical simulations

Numerical simulations of equations 4.4-4.5 confirm the general validity of the analytical findings on asymmetrical and symmetrical migration. However, the simulation results highlight that my analytical approximations from the invasion fitness approach are only accurate when either the proportion of "bad" hosts in the "good" source patch or the performance difference between hosts is small (figures 4.2-4.3). In addition, these simulations go beyond the invasion fitness approach because they allow to identify levels of gene flow where generalist and specialist strategies co-exist in a polymorphic equilibrium and where specialists are thus

more prevalent in sources than in sinks. This finding represents locally adaptive divergence of specialists in core sources and generalists in marginal sinks which, in line with earlier results, is only possible at intermediate migration rates (compare [63]).

4.3.3 Results summary

In summary, the results from my population dynamic model demonstrate that both host abundance and differences in larval performance can lead to source-sink dynamics which limit the success of generalist strategies in heterogeneous environments. In contrast to the optimality approach that predicted spatial heterogeneity to most often lead to generalism, the population genetic model thus identifies a sufficiently high level of gene flow as a necessary condition for generalist oviposition strategies to spread in the population. This is because the source-sink dynamics inherent to spatially varying reproductive success influence the evolution of optimal oviposition strategies in ways unforeseen by pure optimization approaches. Migration increases the selective importance of performance in sinks, but gene flow from sources to sinks also obstructs local adaptation to sinks. As a result, even though the environment is heterogeneous and the optimality model predicts generalism, specialism often remains the evolutionarily stable strategy in the population genetic model. Spatial heterogeneity therefore is only a necessary but not a sufficient condition for the evolution of generalism—it facilitates the rise of generalism but does not automatically entail it.

4.4 Discussion

I use a theoretical model to examine how phytophagous insects may shift evolutionarily from specialist oviposition on a single host to generalist oviposition on all available hosts. I study this question in a system of two habitat patches with divergent abundance patterns of two hosts with different suitability for larval development. While an optimality model maximizing reproductive success predicts generalism to be optimal across a large parameter-subspace, a population genetic implementation of this scenario identifies conditions for the evolution of generalism to be more restricted. This is because spatial heterogeneity in host abundance leads to emergent source-sink dynamics where gene-flow is larger from patches with many "good" hosts to those with many "bad" hosts than vice versa and where there is little natural selection for performance in sinks. As a result, individuals often do not adapt locally to conditions in the "bad" patches—i.e., conditions in those newly emerged sinks where generalist acceptance of both hosts would be optimal—unless differences in performance are small or migration rates are large.

4.4.1 Sources, sinks, and fundamental niches

In line with my results, previous theoretical work has shown that adaptation to conditions in sinks is hardly expected. On the one hand, natural selection on performance in sinks is weak since most individuals hail from sources [65]; on the other hand, asymmetric gene flow from highly productive sources to less productive sinks tends to swamp local adaptation in sinks [62]. These two effects of source-sink dynamics work in the same direction—against local adaptation to sinks and against maintenance of stable antagonistic polymorphisms between sources and sinks. Conceptually, these effects form an example of what McNamara and colleagues termed "adaptive optimism" [75] with animals adapting to better-than-average conditions in sources instead of to average conditions in sources *and* sinks. In the general

context of source-sink dynamics, my results exemplify how high migration rates may increase the selective relevance of performance in sinks while, at the same time, preventing the maintenance of stable polymorphisms between generalism in sinks and specialism in sources.

Spatial heterogeneity has been identified as a central factor in the evolution of ecological niches. This is because adaptation to marginal habitats, where environmental conditions differ from a species' core distribution, may shift ecological niches over evolutionary time [63]. In turn, the definitions of "fundamental niche" and the concept of sources and sinks are tightly linked, though they were coined more than two decades apart [49, 88]. Habitats where a species can reproduce self-sufficiently—i.e., at reproductive rates larger or equal than one—are considered to be *within* a species' fundamental niche, other habitats are *outside* this niche. By definition, all sinks thus lie outside a species fundamental ecological niche, and evolution in sinks may therefore drive the dynamics of ecological niches as well as of species ranges [63].

In this context, my findings are in line with earlier results that predict adaptive evolution within the fundamental ecological niche even at cost outside this niche [44]—in my case the maintenance of specialism in the "good" patch at the cost of not reproducing in the "bad" patch. Effectively, this scenario resembles that of an allele with antagonistic environmental effects where the direction of selection changes between habitats. In such cases, allele frequencies are expected to evolve such as to maximize average reproductive success [67]. In the current case, generalism delivers the highest average reproductive success in the optimality model, but source-sink dynamics lead to predominant specialism in the population genetic model. This insight highlights how the evolutionary emergence of generalism from specialism in phytophagous insects can be a question of adapting to marginal habitats, potentially outside of a species' fundamental ecological niche.

4.4.2 Model assumptions and their consequences

With respect to the genetic architecture of locally adaptive traits, the results presented here likely give a conservative estimate of how spatial heterogeneity can facilitate the evolution of generalism. This is because all traits are automatically "dominant" in this haploid model, and dominance is known to make adaptation to marginal habitats more likely [67]. Moreover, my model of a single locus with (potentially) large effect necessarily excludes linkage disequilibrium or recombination, which could otherwise facilitate local adaptation [64, 67]. As a result, enlarging my model to diploidy or to more loci would likely shrink the parameter subspace where generalism is adaptive.

Similarly, my implementation of dispersal as passive is likely to yield conservative estimates of the conditions for the evolution of generalism. Dispersal plays a manifold role in the evolution to conditions in sinks, not only because gene flow and local adaptation are well-known adversaries [67] or because asymmetric dispersal may create source-sink dynamics in the first place [65]. Dispersal also makes adaptation to new conditions possible by bringing species into new habitats [46] and may sustain otherwise extinction-bound sink populations [9]. But since dispersal potentially exposes individuals to unfavorable conditions, dispersal strategies themselves are subject to evolutionary change. Specifically, spatial heterogeneity is expected to reduce dispersal because animals avoid settling in marginal habitats [43, 45, 62]. As a result, taking into account dispersal strategies such as sink-avoidance would likely further restrict the conditions for adaptation to sinks and thus for the evolution of generalism in my model scenario.

Larval survival rates play a key role in the fitness costs and benefits of specialist and

generalist oviposition strategies. The model presented here takes the survival rates of larvae as a fixed input to insect optimal oviposition strategies. Over evolutionary time, however, larval performance itself is an evolutionarily flexible trait. For example, host plant diversity of two species of *Papilio* butterflies has been shown to relate directly to the specificity and efficiency of these butterflies' detoxifying cytochrome P450 monooxygenases [69]. Conversely, the detoxification capabilities of pierid butterflies are thought to represent an *ancestral* feature of their metabolism *prior* to the switch to host plants that necessitated these capabilities [107].

My reasons for choosing to disregard the co-evolution of larval performance with host acceptance and thus to model only host acceptance behavior are three-fold: First, it seems sensible to suppose that behavioral traits such as host acceptance can change quicker and are less constrained in their flexibility than metabolic traits such as the detoxification of specific plant compounds. Second, modeling the evolution of new and/or altered capabilities to metabolize plant toxins would require a host of additional assumptions regarding, for instance, the chemical similarity of different host plant species as well as the specificities of the metabolites they contain. And third, since evolution of increased larval performance is trivially beneficial unless some costs are involved, such a modeling approach would necessitate assumptions on the specific trade-offs between larval performance on chemically different host species—a topic that is under past and present debate as the so-called 'Jack of all trades, master of none'-principle [32, 34, 92]. Since knowledge on how the detoxifying cytochrome P450 systems of phytophagous insects have co-evolved with different specialist or generalist feeding behaviors is accumulating (e.g.[69, 102]), taking the evolution of host plant detoxification into account may present subject for insightful future study.

4.4.3 Empirical significance

Gene flow and local adaptation

A large body of empirical literature exists on the interplay of gene flow and local adaptation, but few studies explicitly consider the effects of source-sink dynamics. Marginal habitats have been shown to usually contain lower population densities than core habitats (e.g. 99, 119), and source-sink dynamics between cores and margins have been demonstrated to result in asymmetric gene flow in the field [72]. More importantly, such source-sink dynamics have been shown to interfere with local adaptation in plants, insects and birds, both in the wild and in the lab [7, 8, 73, 100, 120].

Most relevant to the case presented here are experiments with *Drosophila melanogaster*, where gene flow counteracts local evolutionary changes in oviposition preference [6], and with the weevil *Callosobruchus chinensis*, where productivity differences that were due to interspecific competition lead to weevils becoming better adapted to more productive hosts [108]. Taken together, these empirical findings are, at least in part, in support of the model's predictions that gene flow and source-sink dynamics are likely to interfer with the evolution of generalism as a response to spatial heterogeneity.

Preference-performance correlations

Since emergent generalism would entail that insects no longer oviposit preferentially only on hosts optimal for larval performance but indiscriminately on all hosts, the results presented in this chapter contribute to the long debate on the presence or absence of correlations be-

tween adult preferences and larval performance [29, 110]. Currently, available empirical data on the subject suggests that preference-performance correlations are the exception rather than the rule [39]. Previous analyses have explained the occasional absence of such correlations by invoking, among others, both spatio-temporal variation in host availability and the influences of insect time-energy budgets [90, 115]. This chapter adds to these results by demonstrating how, in a model scenario that combines spatial heterogeneity and strategic oviposition, preference and performance may be decoupled as a result of adaptation to marginal habitats when migration rates are high (compare figure 4.3).

Diet breadth evolution

Explaining the association patterns of phytophagous insects and their plant hosts necessitates oscillations in diet breadths (see chapter 1 and [54]). The results presented here suggest, however, that the associated increases in diet breadths—the repeated emergence of generalism from specialism—are hard to explain evolutionarily through spatial heterogeneity unless performance costs on suboptimal hosts are low or host abundance patterns change drastically. Spatial heterogeneity alone is therefore not a sufficient condition for the evolution of generalism. Instead, metapopulation structure and migration rates between patches determine whether generalism evolves at all and whether it replaces specialism locally or globally.

4.4.4 Conclusion

In summary, this chapter highlights how adaptation may be limited by the eco-evolutionary feedback that is induced by emergent source-sink dynamics. This finding emphasizes the usefulness of eco-evolutionary approaches for studying the evolution of species associations in spatially varying environments, as has been demonstrated empirically in evolving heterogeneous meta-communities [118]. Only in this way can one take into account the complex interplay of gene flow and local adaptation in emergent source-sink systems and examine the complex feedback of ecological and evolutionary processes that can occur in these situations.

5 Does phenological specialism lead to oviposition generalism in a butterfly?—A simulation approach

Chapter summary

Generalist strategies are only the result of spatial heterogeneity under restrictive conditions (see chapter 4). Yet, diet breadth increases must necessarily have occurred repeatedly over evolutionary time. In the search for other reasons for the evolution of generalist oviposition strategies, the orange tip butterfly (*Anthocharis cardamines*) represents a promising case study. Orange tip larvae are phenological specialists feeding primarily on mature seed pods, but adult females are oviposition generalists accepting a range of cruciferous hosts. Previous work put forward the hypothesis that the larvae's phenological specialization has led to the evolution of the adult females' generalist oviposition behaviors. To explore this hypothesis, I develop an individual-based simulation model where insects encounter different host species whose quality varies in terms of larval performance or carrying capacity and whose abundance changes in seasonal patterns. The simulation results demonstrate that phenological specialism can indeed lead to oviposition generalism. This is because the shorter time windows across which a given host species is suitable for oviposition for a phenological specialist decrease the perceived availability of suitable hosts, so that including lower-quality hosts into the oviposition spectrum becomes profitable. Moreover, the simulations demonstrate that competition between larvae on hosts is likely to have a larger effect on host acceptance rates than differential larval survival. These results are discussed in the context of available empirical findings on orange tip oviposition and of the central role for patterns of environmental variation in insect oviposition. Finally, I present possible future extensions to the simulation, especially regarding the potential of individual-based simulations for use in more cognitivist approaches to strategic oviposition in insects.

5.1 Introduction

The evolution of generalism from specialism remains a puzzle in insect ecology. For detoxification reasons, insect larvae are likely to perform differentially well on different host plant species. This prediction is known as the 'Jack of all trades—master of none'-principle, which predicts a trade-off in performance between different host plants (e.g. [32], but skeptic views exist on the generality of this principle—[34, 92]). As a result, the question remains why a female should evolve to lay eggs on a low-quality host where her larvae are less likely to survive, even though higher-quality hosts with better chances of larval survival are also present? The great majority of butterflies, for instance, are relatively restricted in the number of host species that they lay eggs on. Phylogenetic analysis suggests that no single ancestral generalist has radiated into the many specialists in existence today. Instead, ancestral specialists

likely gave rise to more widespread generalists that in turn tended to adapt to location conditions and diversify into novel specialists [54]. As a result of these oscillations in diet breadth, the many host switches that must have occurred over evolutionary time necessitate the repeated evolution of generalist oviposition strategies.

But what exactly are the conditions that favor the evolution of a more generalist diet breadth that includes possibly suboptimal hosts? The orange tip (*Anthocharis cardamines*) is a pierid butterfly that represents an insightful example for this case. Its larvae are phenologically specialized in that they usually do not consume leaves but only flowers and especially mature seeds [20, 126]. Adults show concordant oviposition preferences for hosts with sufficient inflorescences of appropriate age to supply larvae with enough mature seed pods [126]. At the same time, the orange tip butterfly is an oviposition generalist in that adults lay their eggs on a wide variety of cruciferous plants, ranging from its namesake *Cardamine pratensis*, the widespread cuckoo flower, to the model organism *Arabidopsis thaliana* [126].

The goal of this chapter is to explore the hypothesis that phenological specialism of orange tip larvae on mature seed pods has led to more generalist oviposition strategies of adult female orange tips [127]. In particular, specializing on one phenological state of their host plants—namely when mature seed pods are present—leaves only a short time window for successful reproduction. Including hosts into the diet breadth that flower earlier or later than the ancestral host will increase this time window and may therefore be beneficial. Inspection of the flowering phenology of the different cruciferous host plant species in a Swedish population of *A. cardamines* supports this hypothesis [126, 127]: Compared to the host plant with the highest number of eggs, *Cardamine pratensis*, butterflies also oviposited on host plant species that flowered earlier, such as *Arabidopsis thaliana*, as well as on host plants that flowered later, such as *Thlaspi arvense*. Suggestively speaking, the time windows when the different host plant species are suitable for oviposition seem indeed to be spread out across the flight period of orange tip females.

Regarding the quality of their various cruciferous hosts, orange tip larvae have been demonstrated in the field to perform differentially well on the different plant species of their host spectrum [127]. Total survival varied from 9–12% on relatively good hosts (e.g. *Capsella bursa-pastoris* or *A. thaliana*) to 3–5% on less good hosts (e.g. *C. pratensis*) and even down to 0% on bad hosts (e.g. *Draba muralis*—[127]). Larval survival was found to vary strongly on the same host plant species between years, which can be attributed to factors external to specific host plant species such as predation by parasitoids, host dessication after drought, or drowning of larvae after heavy rains [127]. Nonetheless, these results confirm that host plants differ in their quality for larval survival, even though the hosts' relative rankings may shift between years. However, host plant utilization by females was only poorly matched to host-species-specific larval survival [127].

Overall, the data availability on plant characters and their phenology as well as on butterfly oviposition makes the orange tip a promising study system, especially in combination with the adult females' generalist oviposition strategies. Nonetheless, to my knowledge there have been no previous modeling attempts explicitly aimed at the orange tip's oviposition behavior. In this chapter, I thus aim to develop a model of strategic oviposition that takes into account acceptance rates and larval performances on different host plant species in order to examine evolutionary changes of the insects' diet breadth in response to temporal constraints in host availability. To do so, I create a simulation model of insect oviposition that considers egg-laying behavior in an explicitly seasonal context where the availability of different host species may change over the course of the season. I perform a number of

simulations to assess the roles of larval performance and larval competition in determining optimal oviposition strategies and compare these results to the conclusions from previous chapters' analytical models. Finally, I present simulation results that test whether, indeed, smaller time windows of host availability can lead to the acceptance of lower-quality hosts into the insects' diet breadth.

5.2 Model description

The following description of my individual-based model of insect oviposition follows the helpful ODD-protocol (Overview, Design concepts, Details) for describing individual-based models proposed by Grimm and colleagues [38].

The model was written in C++ using the Eclipse IDE for C/C++ developers (`http://eclipse.org`) and the g++-compiler as provided within Minimalist GNU for Windows (`http://mingw.org`). The structure of the program and parts of the code are based on an unpublished simulation model on the evolution of larval performance on different host plants by Olof Leimar. Analysis of the results was conducted in R v 2.13.2 (R Development Core Team, 2011) using RStudio 0.95.262 (RStudio, Inc., 2011).

5.2.1 Overview

Model purpose

The purpose of the model is to understand how the availability of suitable hosts over the course of a breeding season shapes the oviposition preferences of female butterflies. In particular, the model aims to identify ecological circumstances where insects may incorporate hosts of lower-quality into their oviposition spectrum—that is, circumstances where insects adopt more generalist oviposition strategies.

State variables and scales

The model comprises four hierarchical levels: individual, patch, metapopulation, and environment. Individuals are described by their genotype, their phenotype, the identity number of the patch where the individual hatched, and the season period when their egg of origin was laid by their mother. An individual's genotype consists of one diploid locus where each allele has a k-dimensional real value with k corresponding to the number of different host plant species under consideration. An individual's phenotype consists of a k-dimensional vector of probabilities with which this individual accepts for oviposition the k different host plant species. The phenotypic vector of host acceptance rates follows from the genotype by simple addition of the two component allelic values.

A patch may be occupied by a number of individuals up to a set carrying capacity. Each patch is thus characterized by its patch identity number and the number of individuals present. The patches are organized in a large metapopulation, which is described by the number of patches it comprises. Within the metapopulation, individuals can move between patches by first being transferred to a global migrant pool with a certain migration probability and then being randomly transferred to a different patch from this global pool. In the current simulations, population structure was not an aspect under study, but the patch structure of the environment was retained for computational reasons (different patches could be

processed in parallel, which decreases computation times). Therefore, migration rates were generally set very high (at 90%) to achieve a well-mixed metapopulation.

The environment in this model represents the seasonally varying ecological conditions that the insects are facing. Since the availability of suitable hosts is the most important aspect in optimal insect oviposition, the environment in the model is characterized by this factor. The environment is structured in such a way that each reproductive season consists of a number of periods, here varied between 1 and 20. For each period and each host species, host availability is then given as the abundance of that host species during that period.

Process overview and scheduling

In its population dynamics, the model proceeds in time steps that correspond to one reproductive season. The oviposition dynamics of the individuals, however, take place on a shorter time scale within the periods of that season (see section 5.2.3). Within each reproductive season, five steps are processed for each patch in the following order: (1) emigration to the global migrant pool, (2) immigration from the global migrant pool, (3) reproduction and oviposition within the patch, (4) survival selection among larvae, (5) competition among surviving larvae on given host plant species in patch. This life cycle is shown in figure 5.1.

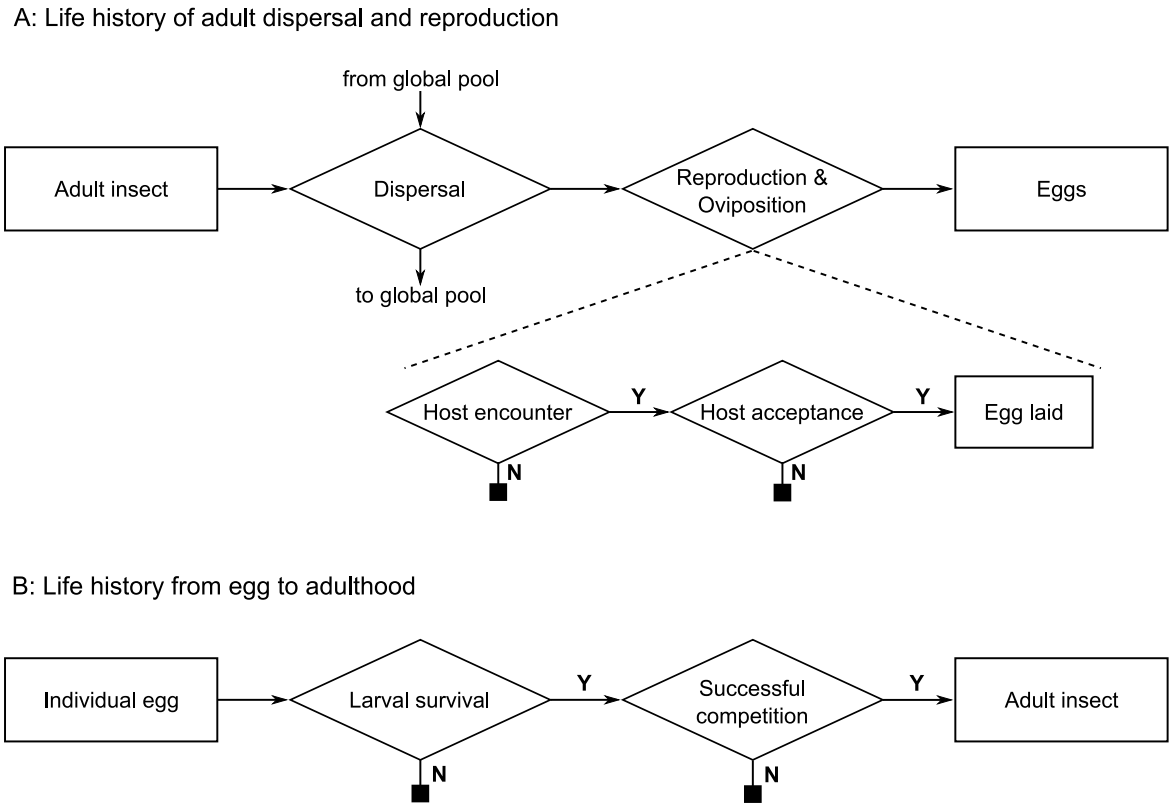


Figure 5.1. Life history of the individual insects as modeled in the simulation study. Panel A depicts the life history of an adult insect dispersing and reproducing with the inlay showing the act of oviposition. Panel B shows the life history of an insect from egg to adulthood. Figure adapted from an example given in [38].

5.2.2 Design concepts

Emergence: Population dynamics emerge from the oviposition strategies of the individuals. These strategies are in turn entirely represented by the acceptance rates encoded by the individuals' genotypes. These genotypes change by random mutation (see section 5.2.3), and altered acceptance rates may result in higher or lower reproductive success. As a result, adaptation, though not modeled explicitly, emerges from the differential reproductive success of individual, genetically determined oviposition strategies. As a result, the relative frequencies of alleles coding for different acceptance rates change over time, and the average acceptance rates of different host species vary over the course of a simulation run.
Sensing: For every host encounter, individual insects are assumed to know the species of this host, so that they can apply the "correct" phenotypic acceptance rate in the immanent oviposition decision.
Stochasticity: All oviposition decisions are interpreted as stochastic, where an individual will accept a given host for oviposition upon encounter if a number drawn from a uniform distribution between zero and one falls on or below the individual's acceptance rate for that host species. Host encounter is modeled as a Poisson process where individuals encounter plants of a given host species at a constant given rate, which is assumed to be equal to that host species' abundance in the given patch in the given season period. Host encounters are thus Poisson distributed with mean number and variance of encounters with a given host species equal to that species' abundance.
Interaction: There is only indirect interaction among insects in that surviving larvae compete for space within the population of a given host species in a given patch in a given season (see section 5.2.3). No direct interaction among ovipositing females is taken into account.
Observation: Of all surviving individuals of the final generation of each simulation, I recorded for model analysis each individual's genotype, phenotype, patch of origin, host plant species of origin, and season period of origin.

5.2.3 Details

Initialization

The environment was initialized from input data on host abundance given by the experimenter for each host species and each season period. Since the simulation's focus was not on the effect of population structure (see above), host abundance was assumed to be equal across all patches (but not across all periods of a given reproductive season). Each patch was then filled up to carrying capacity with individuals with an initial genotype where acceptance of all host species was random. That is, for each individual, phenotypic acceptance rates were set to 0.5 for all host species by setting the genotypic value at each dimension of the two k-dimensional alleles to 0.25.

Input

Data given as inputs to the model included numbers of generations, patches, and host plant species to simulate; number of periods per reproductive season; host abundances for each host and season period; larval survival rate on each host plant species; carrying capacity of each host species per abundance unit and patch; maximum number of eggs laid during a lifetime (i.e., fecundity); migration probability; initial host acceptance rates as well as minimum and maximum values for these quantitative traits; mutation probabilities as well

as a scaling factor for the mutation increments; maximum host encounter rate per simulation time step (see below for details). These parameters are summarized in table 5.1.

Table 5.1. Overview of the parameters as well as their default values and ranges in the oviposition simulation.

Parameter	Value / Range
General parameters	
Number of generations	1000
Number of patches	100
Number of host plant species	1–2
Number of periods per season	1–20
Migration probability	0.9
Host encounter & oviposition	
Host abundance per host species and period	0.1–20
Fecundity (number of eggs)	2–20
Maximum host encounter rate per time bin	0.05
Initial genotypic value for each host species	0.25
Resulting initial acceptance rate for each host species	0.5
Larval survival on given host species	0.05–1
Carrying capacity per host species abundance unit and patch	0.1–10
Mutation	
Mutation probability	0.05
Scaling parameter for distribution of mutational increments	0.05
Trait minimum and maximum values for each allele	0.0, 0.5

Submodels

For the default values or ranges of the parameters mentioned in the submodel-descriptions below, please refer to table 5.1.

Mating and mutation: Reproduction is sexual and mating is random, but true "sexes" are absent from the model. That is, each reproducing individual is assigned a random "paternal" mate from its patch, and each individual only mates once. Mutation occurs during the formation of haploid gametes from each parent, which then fuse to form diploid offspring. Mutation occurs independently for each value of the k-dimensional allele with the given mutation probability. Mutational increments are drawn from a Laplacian distribution with mean and standard deviation 1, rescaled with the given scaling parameter.

Insect fecundity: Each individual lives through all periods of a single reproductive season. An individual's fecundity is divided evenly among the periods of that season. If total fecundity divided by season length leaves a rest x, then fecundity in the season's first x periods is increased by one. This is because an individual cannot lay its entire egg complement within a single season period, but instead can only lay a certain fraction of its eggs within each period of a given season.

Host encounter: In order to implement random Poisson encounters with the different host species, time within a given season period was binned adaptively so that the maximum

encounter rate with each host species in that period does not exceed a certain threshold, generally set to 0.05. As a consequence, I disregarded the potential of multiple encounters with the same host species within a single time bin, the likelihood of which would have been at most $\sum_{k=2}^{\infty} 0.05^k \approx 0.0026$.

Oviposition: Upon encountering a host of a given species, an individual insect accepts this host for oviposition if a random number drawn from a uniform distribution between zero and one falls on or below the individual's acceptance rate for this host species. I considered only one such successful oviposition per time bin.

Larval survival: A given egg on a host plant of a given species survives to adulthood if a random number drawn from a uniform distribution between zero and one falls on or below the value of the larval survival rate for that host species.

Competition among surviving larvae: The population of hosts of a given species only supplies sufficient resources for a given number of surviving adults—i.e., up to that host species' total carrying capacity in the given patch. This maximum number of surviving adult insects is estimated by multiplying the carrying capacity of that host species *per abundance unit* with its summed abundance over all periods of the reproductive season. Then, egg survival to adulthood is tested in random order until this total carrying capacity is reached (or until all eggs have been tested).

5.3 Effects of larval performance, larval competition, and host abundance

For better readability, I have divided the simulation results into two sections. The first part, presented in the current section, deals with the effects of larval performance, larval competition, and host abundance on strategic oviposition. The second part, presented in section 5.4, focuses on the effects of seasonal host abundance patterns on oviposition strategies.

5.3.1 Effects of larval performance

Assume an insect species that can lay its eggs on two different host species but whose larvae fare better on one than on the other host. That is, the chances of larvae hatched from an egg surviving to adulthood differ between the hosts—there is differential larval *performance*. For simplicity, I will assume a single performance index that describes the probability of survival from egg to adulthood on a host species due to larval performance on that host.

In a situation like the one presented above, I have learned from the optimality model that acceptance rates, the probability that an insect will lay an egg on a given host species upon encounter, depend critically on larval performance on that host (see chapter 4). This is because lower larval performance on a given host species reduces the payoff in terms of reproductive success gained from each egg laid on that host. Following this approach, insects are expected to show higher acceptance rates for hosts where their larvae perform better compared to hosts where their larvae perform worse. Indeed, the optimality model demonstrates that lower-quality hosts are only accepted when they are abundant and higher-quality hosts rare (see figure 4.1 on page 44 of chapter 4).

When we transfer the situation to the individual-based simulations, we might expect an even stronger effect of larval performance on adult oviposition preference. This is because, in the optimality model, adults were assumed to die with a specific mortality rate so that rejecting low-quality hosts may carry the cost of not being able to lay all eggs during one's

lifetime—the familiar case of *time limitation*. This effect reduces the benefit of not laying eggs on low-quality hosts because such behavior now carries an opportunity costs in terms of potentially unlaid eggs. In contrast, the simulation model takes mortality to be low enough for us to assume that females always survive the entire breeding season. As a result, the opportunity cost of rejecting a low-quality host is greatly reduced, and we would expect females to show clear preferences for higher-quality hosts. In fact, when staying with the example of only two host species, we may even expect a clear switch between always rejecting the lower-quality host and always accepting the higher-quality host. This is because, naturally, fitness returns per egg are higher on that host species which shows higher larval performance. If you were to deposit a sum of money at one of two banks, you would gain most by depositing the entire amount at the bank that offers highest interest rates, not by splitting the amount between the two banks (all else being equal, of course).

Initial analysis of the simulation results runs counter to these expectations. When I take one host species to have constant high larval performance but vary performance on the second host species, insects only show a clear preference for the first host if performance on the second host is very low (see figure 5.2, first row). Why this is the case will be examined in detail in the next subsection.

Insects become slightly more choosy in their oviposition behavior and reject the lower-quality host already at slightly higher, but still low, larval performance if their lifetime fecundity is lower (compare left and right panel in first row of figure 5.2). This finding demonstrates that the statement given above—that opportunity costs of host rejection vanish completely—was slightly oversimplified. In order to see why this is the case, consider that the simulation takes insects to encounter a certain number of hosts per mating season and to carry a certain number of eggs. Oviposition is therefore likely limited by eggs if the average number of eggs is below the average number of host encounters, and limited by hosts if the opposite is the case. As a result, the opportunity costs of rejecting a host for oviposition increases as the number of eggs approaches the average number of host encounters per season. Still, the correlation between preference and performance is much lower than would have been expected from the previous chapter's optimality model.

5.3.2 Effects of competition for survival among larvae

As a deeper analysis of the simulation model shows, the unexpected absence of preference-performance correlations is due to competition among the larvae on a given host species. While the optimality model did not consider such intraspecies competition, the simulation model assumes that each host species has a specific carrying capacity and cannot support more surviving larvae than this capacity. This carrying capacity can differ between host species, and the total carrying capacity of each host species scales with the abundance of that host. As a result, the chances of an egg surviving to adulthood on a given host species depends not only on larval performance on that host but also on the total amount of larvae on that host relative to its total carrying capacity.

A simple mathematical approximation illustrates why competition can lead to the disappearance of preference-performance correlations. In order to survive to adulthood, a larva has to perform successfully on a given host *and* has to emerge successfully from competition with the other surviving larvae. The probabilities of achieving either task are independent and can thus simply be multiplied. More importantly, the probability of successful performance scales linearly with the larval performance parameter, whereas the probability of successful competition scales inversely with this parameter—when less eggs manage to "per-

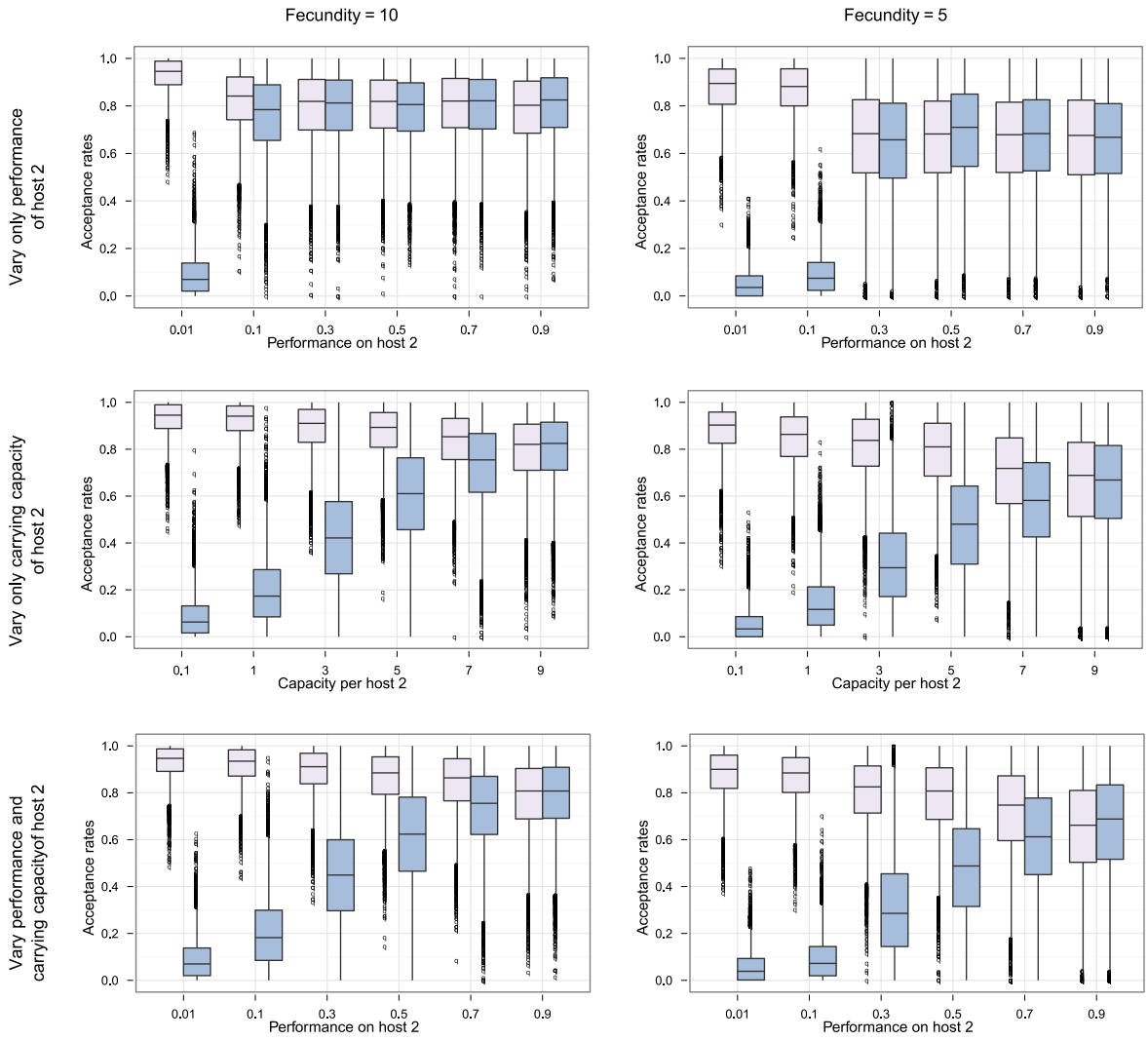


Figure 5.2. Effects of performance and competition on oviposition preferences. Acceptance rates for a lower-quality host (darker shade) and one of constant higher quality (lighter shade) as a function of the quality of the lower-quality host. Host quality is varied in terms of larval performance (first row, performance of higher-quality host constant at 0.9), in terms of carrying capacity per abundance unit (second row, capacity of higher-quality host constant at 9), or in terms of both performance and capacity (third row, combination of treatments in first and second row). Simulations were run with insects possessing either 10 or 5 eggs at eclosion (left and right column), and insects encountered on average 10 hosts of each host species per season. Simulations were run for 1000 generations in 100 well-connected patches (migration rate of 90%) with a total carrying capacity of between 101 and 200 per patch (depending on capacity of the lower-quality host as varied above).

form", there will be less competition among the remaining larvae. In fact, if competition is random and the number of larvae is higher than the host's carrying capacity, the chances of surviving competition on a given host species are simply the carrying capacity of that host divided by the number of surviving larvae on that host which, in turn, corresponds to the number of eggs laid on that host multiplied with these eggs' average performance. As a result, multiplying the probability of successful performance with that of successful competition lets the influence of larval performance on survival probability disappear from the equation:

$$
\begin{aligned}
\text{Prob. of survival} &= \text{Prob. of successful performance} \cdot \text{Prob. of successful competition} \\
&= \text{Larval performance} \cdot \frac{\text{Total carrying capacity on host}}{\text{Number of larvae on host}} \\
&= \text{Larval performance} \cdot \frac{\text{Total carrying capacity on host}}{\text{Number of eggs on host} \cdot \text{Larval performance}} \\
&= \frac{\text{Total carrying capacity on host}}{\text{Number of eggs on host}}
\end{aligned}
$$

The simulation results support this intuition. When two hosts species differ in their carrying capacity but not their larval performance, insects show a higher acceptance rate for the host with the higher carrying capacity (see figure 5.2, second row). That is, insects prefer that host species where there is less competition among eggs for survival. This finding represents a more indirect version of preference-performance correlations since, in this scenario, differential larval survival is not due to differences in larval performance but to differences in density-dependent competition on each host species. Of course, when the two host species differ both their carrying capacity *and* their larval performance, insects still show higher acceptance rates for the host with the higher carrying capacity (see figure 5.2, third row).

As before, insects become more choosy in their oviposition behavior as their fecundity decreases because this increases the opportunity cost of laying eggs on low-quality hosts (compare left and right column of second and third row of figure 5.2). Additionally, as acceptance rates of the host with the lower carrying capacity decrease, those of the host with the higher but unchanged capacity increase (see figure 5.2, second and third row). This is due to the constraints set on oviposition by the limited number of hosts encountered during one season. Simply put, a female insect that becomes less likely to accept one host species should become more likely to accept the other in order to still be able to lay all her eggs.

5.3.3 Effects of host abundance

Finally, instead of varying host carrying capacity, I can also vary host abundances, thereby changing the encounter rates of female insects with these hosts. If, among two host species, one is more rarely encountered than the other but offers the same payoff in terms of reproductive success, females are not expected to show a preference for either host. Simulations

results show that this is indeed the case, at least when the rarer host is still reasonably abundant (see figure 5.3). As the less abundant host becomes increasingly rare, however, average acceptance rates of that host decrease (see figure 5.3). This is because selection for increased acceptance of the rarer host is inefficient if that host is encountered so rarely. Therefore, average acceptance rates may not increase significantly beyond the initial value of 0.5 (i.e. random acceptance) and only the variance of acceptance increases due to mutational noise. In accordance with this idea, the pattern of acceptance rates does not change if simulations are run for 10000 instead of 1000 generations (data not shown).

Additionally, when host abundances are varied, total host encounter rates shrink if one host becomes less abundant while the other host's abundance stays constant. Since females are thus more likely to be limited in their oviposition by the number of hosts they encounter than by the number of eggs they carry (see above), acceptance of the more common host increases as the less common host becomes increasingly rare. Similarly, decreasing fecundity leads to lower average acceptance rates of both hosts when they are common (compare left and right column of figure 5.3) because, simply put, a lower number of eggs means that all eggs can be laid at lower average acceptance rates than if one had more eggs.

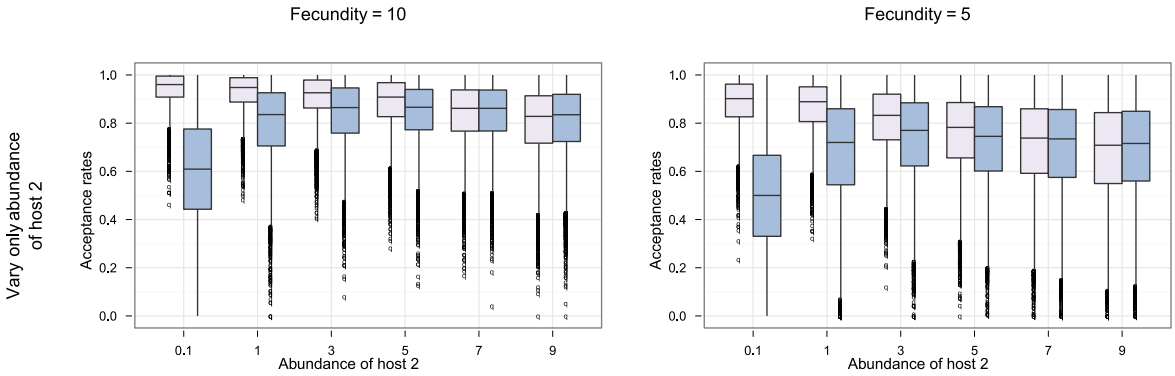


Figure 5.3. Effect of host abundance on oviposition preferences. Acceptance rates for a less abundant host (darker shade) and one of constant higher abundance (lighter shade), both of equal quality for larval development, as a function of the abundance of the rarer host. Simulations were run with insects possessing either 10 or 5 eggs at eclosion (left and right column), and insects encountered the common host on average 9 times per season. Simulations were run for 1000 generations in 100 well-connected patches (migration rate of 90%) with a total carrying capacity of between 91 and 180 per patch (depending on abundance of rarer quality host as varied above).

5.3.4 Effects of host limitation

When there are fewer hosts in total but insect fecundity remains unchanged, each female is more likely to be limited by the number of hosts it encounters than by the number of eggs it carries (see above). As a result, insects should become less choosy in their host acceptance strategies as host abundance decreases. In order to test this effect, I manipulated the abundance of two host species of different quality so that both hosts are equally abundant but their combined abundance varies. This approach contrasts with the treatment presented in figure 5.3 where I varied only the abundance of the lower-quality host but did not change

the abundance of the higher-quality host.

The results confirm my expectations: As the abundance of each host shrinks, acceptance rates of the lower-quality host increase (see figure 5.4, top two rows). This result holds when host quality varies either in terms of larval performance or in terms of carrying capacity. As expected, the effect of reduced host encounter is more pronounced when quality differences between hosts are larger. Moreover, the results for large quality differences suggest a threshold effect where, below a certain host encounter rate, insects switch from a specialist to a generalist strategy. This is in line with the expectations derived from the optimality model where such threshold behavior is observed as well (see figure 4.1 on page 44 of chapter 4).

In order to examine the relationship between host encounter rates and fecundity further, I varied both these parameters at the same time while keeping their ratio constant. This treatment is not expected to affect optimal oviposition strategies because the relative effects of host- or egg limitation depend on the ratio between fecundity and the average number of host encounters in a lifetime. The results presented here confirm this intuition with host acceptance rates remaining largely unchanged (see figure 5.4, bottom row).

5.3.5 Results summary and outlook

Taken together, these results on host limitation play an important role when examining whether phenological specialization may lead to insects evolving wider diet breadths. For instance, a seed pod specialist would do well to lay its eggs only on hosts with sufficient mature seed pods, whereas a leaf-eating species can lay its eggs on all hosts with sufficient leaf area. Since hosts with sufficient mature seed pods are available during a shorter time window than hosts with sufficient leaf area, this difference in phenological specialization will translate to a reduced encounter rate of suitable hosts. Simply put, a seed-specialist will encounter fewer suitable hosts of a given host species than a leaf-specialist whose larvae feed on the same host species. The results presented above show, however, that reduced host encounter rates *as such* can already lead to changes in optimal oviposition strategies. As a result, assessing the effect of phenological specialization on optimal oviposition may require separating the direct effect of lower host encounter rates from more indirect effects like decreased temporal reliability of suitable hosts.

5.4 Effects of seasonal host abundance patterns on oviposition strategies

In natural habitats, insects are faced with seasonal environments characterized by yearly-repeating patterns. For instance, some host species appear early in the season and flower early, while others may appear late and flower late (see [126, 127], as discussed in section 5.1). As a result, insects are faced with a varying amount of suitable hosts over the course of a given breeding season. This section examines the effects of such seasonal patterns of host occurrence on the insects' oviposition strategies.

In order to examine such seasonal scenarios, I run simulations where each season has a certain amount of periods with potentially different host abundances during each period. In essence, this corresponds to a situation where the breeding season can be divided into a certain number of sections with constant abundance of suitable hosts during each section.

5.4.1 Effect of host distribution patterns on accept-

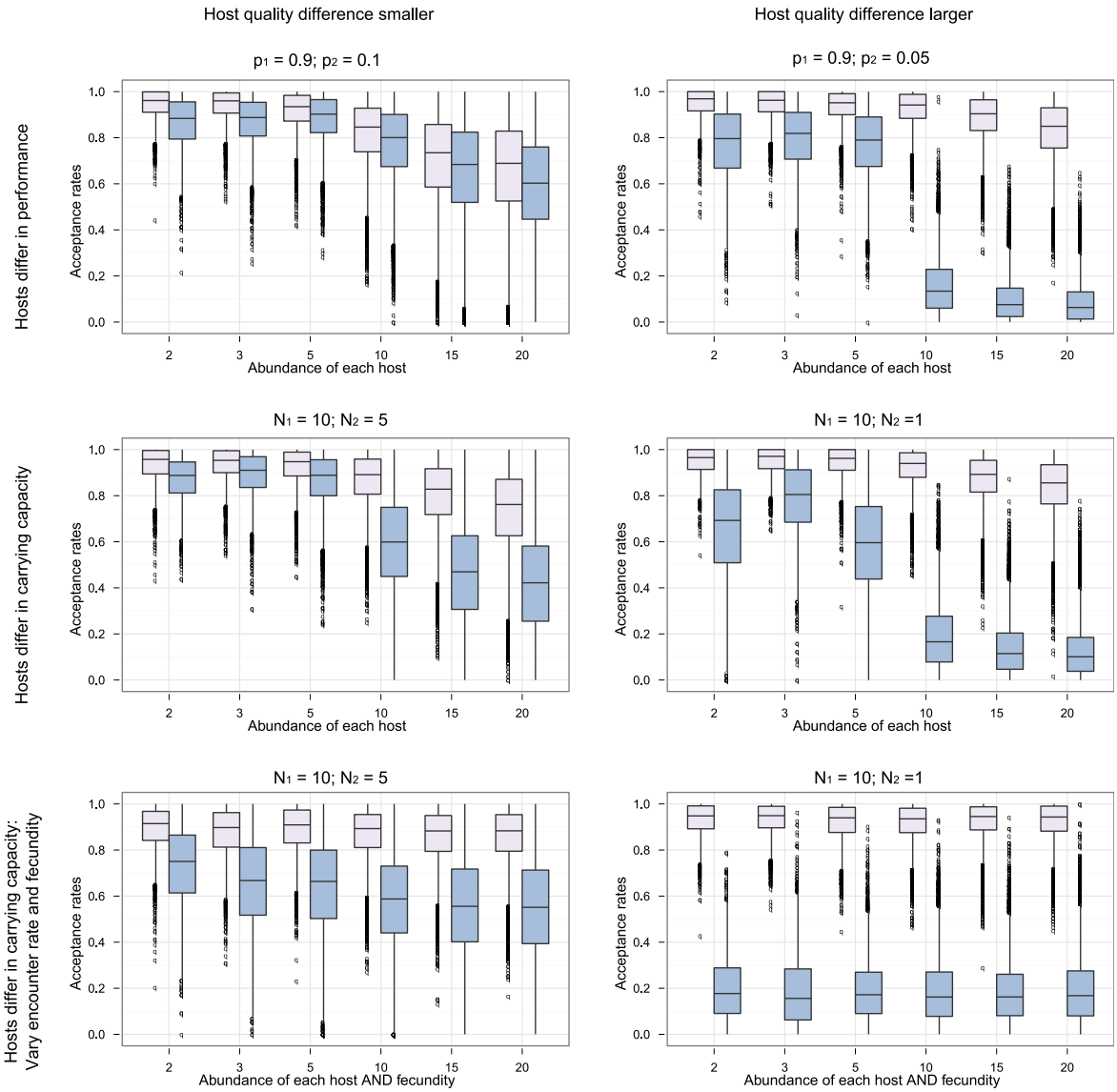


Figure 5.4. Effects of combined host abundance on oviposition preferences. Acceptance rates for a lower-quality host (darker shade) and a higher-quality host (lighter shade) as a function of the combined abundance of the two hosts. Host quality is varied in terms of larval performance (first row, performance values as specified above the panels; capacity set to $N_i = 10$ per unit host abundance) and in terms of carrying capacity per unit host abundance (second and third row, capacities as given above the panels; performance set to $p_i = 0.9$). Simulations were run with insects possessing either 10 eggs at eclosion (first and second row) or with fecundity varying alongside abundance (third row). Simulations were run for 1000 generations in 100 well-connected patches (migration rate of 90%) with a total carrying capacity of between 22 and 400 per patch (depending on host capacity and abundance as varied above).

ance rates of host species with equal quality

I begin by examining a scenario where insects can lay eggs on two host species which, for now, differ in neither larval performance nor carrying capacity. Assuming that a season consists of three distinct periods, I vary host distribution patterns across periods so that average total host encounter rates with each host species remain constant at 12 per season. This results in different patterns where abundance distributions can either be equal (i.e., $4-4-4$), skewed (i.e., $8-2-2$ or $10-1-1$ and other permutations), or concentrated to less than three periods (i.e., $6-6-0$ or $12-0-0$ and other permutations).

The results demonstrate that, as expected, insects oviposition strategies do not react to different permutations of the same basic abundance pattern. That is, average acceptance rates do not differ between the distribution patterns $12-0-0$, $0-12-0$, and $0-0-12$ (see figure 5.5, top two rows). Between different basic abundance patterns, however, average acceptance rates rise as host abundances within single periods decrease (see figure 5.5, bottom row). For instance, median acceptance rates of both hosts lie around 65% when all twelve average host encounters occur in only one period but rise to around 90% when these encounters are unevenly divided so that, on average, ten occur in one period and one each in the two remaining periods (see figure 5.5, bottom row).

In order to interpret these data, remember that we do not expect insects to preferentially oviposit on either of the two hosts because these differ in neither larval performance nor carrying capacity. Instead, the changes in acceptance rates in response to different host distribution patterns can most likely be attributed to insects reacting to different probabilities of time or egg limitation (see chapters 2 & 3). Specifically, insects are expected to increase their acceptance rates if the average risk of time limitation rises because, otherwise, they may not be able to lay all their eggs over the course of the breeding season.

At first glance, it may seem unclear why insect oviposition strategies would be affected by host distributions across seasons as long as total host encounter rates remain constant. However, lower host encounter rates in some periods of a season mean that too low acceptance rates are more likely to be penalized by reduced oviposition rates compared to when host encounter rates are higher. As a result, insects demonstrate the highest acceptance rates when encounter rates in one of the three periods is lowest (see figure 5.5, bottom row). This behavior is directly related to the model assumption that insect fecundity is evenly divided across all period of a season (see section 5.2.3). As a result, if very few hosts are encountered during a particular number of periods, host acceptance rates need to increased in order to still lay sufficient eggs in those periods.

On a more general level, this finding is reminiscent of the phenomenon of "adaptive pessimism" (refer back to section 1.4 on page 7 of chapter 1). In essence, this concept suggests, that the geometric nature of reproduction lets lineages faced with temporally varying environments adapt disproportionately to less favorable conditions compared to more favorable ones [75]. Thereby, animals perform a bet-hedging strategy where they decrease the variance in fitness by decreasing their average fitness so that, from the outside, animals seem to behave as though conditions were worse than they actually are. In the case presented here, individual insects seem to adjust their acceptance rates to the conditions in those periods of a season where host encounters occur least frequently.

5.4.2 Effect of host distribution patterns on accept-

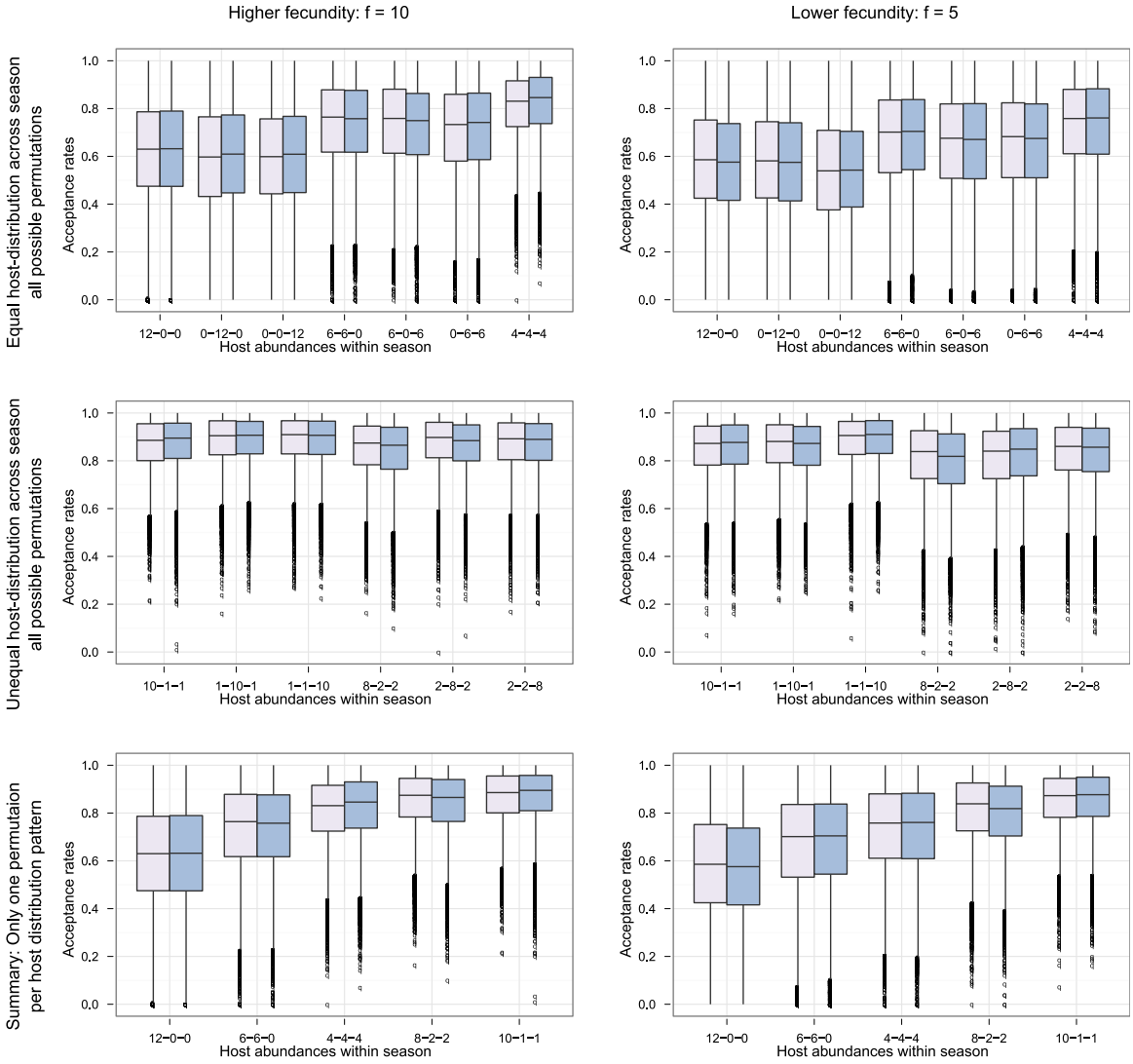


Figure 5.5. Effect of host distribution patterns on acceptance rates of host species with equal quality. Acceptance rates of two host species of equal quality (light and dark shade) for different host distribution patterns across a three-period season. The first and second rows show all possible permutations of each tested host distribution pattern, the third row shows a summary of these data with only one permutation per pattern. Larval performance on both host species was set to 0.9 and carrying capacity to 10; insect fecundity was varied between $f = 10$ (left column) and $f = 5$ (right column). Simulations were run for 1000 generations in 100 well-connected patches (migration rate of 90%) with a total carrying capacity of 240 per patch.

ance rates of lower-quality hosts

As the previous subsection showed, insect acceptance rates of two equally suitable hosts respond evolutionarily to different distribution patterns of these two hosts. Specifically, insects increase their acceptance rates when certain periods of a season are marked by a lower-than-average number of host encounters.

These findings suggest a role for seasonal host distribution patterns also in scenarios when insects are faced with hosts of *unequal* quality. Specifically, seasonal host distribution patterns may influence insect oviposition strategies in such a way that, for some distribution patterns, insects only accept higher-quality hosts whereas, for other distribution patterns, insects also include lower-quality hosts into their host spectra. Judging from the results on equal quality hosts presented above, we would expect season periods with low host encounter rates to lead to higher acceptance of lower-quality hosts.

In order to test this prediction, I ran simulations where insects encounter two different host species that differ in their quality for oviposition, either in terms of their influence on larval survival or in terms of their carrying capacity. I chose these two treatments of quality difference because previous model-analyses showed that insects respond differently in their oviposition strategies to differences in larval survival or carrying capacity (see section 5.3). I then varied seasonal host distribution patterns similarly for the two host species while, as before, keeping constant the average total number of host encounters over the course of a season. For reasons of simplicity, I focused on equal distributions of host encounters over a given season and, therefore, simply varied the number of periods contained in a season. That is, seasonal host distributions were varied between a one-period season with an average encounter rate of 10 per host species and period up to a twenty-period season with an average encounter rate of 0.5 per host species and period.

The results from these simulations confirm my hypothesis. Lower host encounter rates per period are shown to lead to higher acceptance rates of low-quality hosts (see figure 5.6). The resulting changes in acceptance rates, however, are less pronounced that in the case of equal-quality hosts (compare figure 5.5). This finding is due to a fundamental difference between the two cases regarding the fitness costs of different oviposition strategies. When insects are faced with hosts of equal quality, increasing acceptance rates carries no associated fitness costs. When insects are faced with hosts of different quality, however, increasing acceptance rates of lower-quality hosts can carry significant costs in terms of reduced offspring numbers. Moreover, the effect of insect fecundity being divided evenly across all periods of a season necessarily has smaller effects on oviposition strategies if host encounter rates are evenly divided as well.

Quantitatively, the effects of host distribution patterns on acceptance of lower-quality hosts can be examined by comparing the results from the seasonal simulations with those from the single-period cases with varying host abundance (see section 5.3.4). Specifically, while acceptance rates of lower-quality hosts increase with the number of periods in multi-period seasons (figure 5.6), these acceptance rates nonetheless never rise to similar levels as when, in the single-period case, total host abundance is reduced from 10 to 5 (compare figure 5.4, top right and center right panel). In other words, the effect of host distribution patterns in promoting generalist oviposition strategies is comparably small.

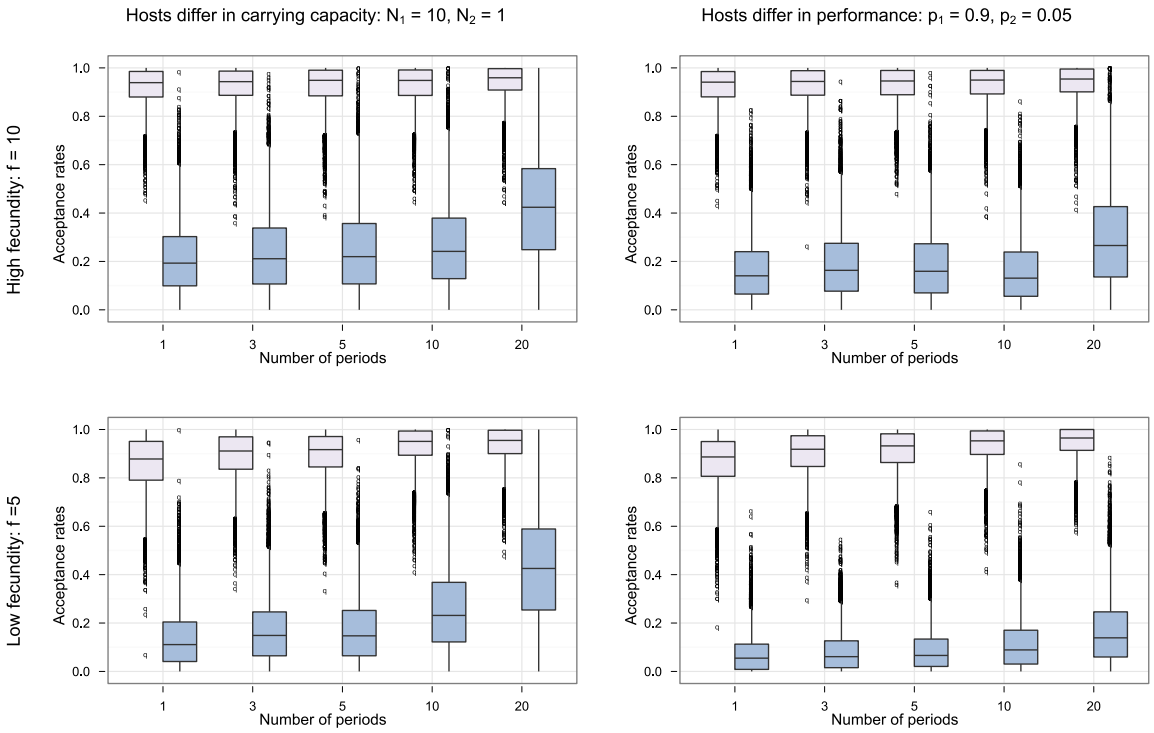


Figure 5.6. Effect of host distribution patterns on acceptance rates of host species with different quality. Acceptance rates of two host species of different quality (light shade, higher quality; dark shade, lower quality) for seasons of different length but with constant average host encounters of ten per host species per season. In the left column, host species vary in carrying capacity with larval performance on both host species set to 1; in the right column, host species vary in larval performance with carrying capacity set to 10 on both host species. Insect fecundity was set to either $f = 10$ (top row) or $f = 5$ (bottom row). Simulations were run for 1000 generations in 100 well-connected patches (migration rate of 90%) with a total carrying capacity of 200 per patch.

5.4.3 Effect of phenological specialization on acceptance of lower-quality hosts

As elaborated in the introduction (see section 5.1), the orange tip butterfly, *Anthocharis cardamines,* shows a comparably wide range of host plants. This oviposition generalism may in part be due to the orange tip larvae's phenological specialism feeding only on mature seed pods and not on plant leaves, in contrast to closely related, less generalist species such as the small white butterfly, *Pieris rapae* (e.g. [47]). Within the life cycle of a given plant, mature seed pods are available during a considerably shorter time window than leaves [126]. As a result, the perceived availability of suitable hosts over the course of a season is lower for a seed pod specialist such as the orange tip than for a leaf specialist such as the small white [127].

As a result, I now examine the case of whether smaller windows of host availability over the course of a reproductive season can lead to inclusion of lower-quality hosts into an insect's oviposition spectrum. To this end, I ran simulations where, as before, individuals are faced with two host species of different quality that vary either in their effect of larval performance on in their carrying capacity. Focusing on a ten-period season, I varied the number of periods with suitable hosts within a given season, letting insects encounter on average one host of a given species in each period where that species is suitable. In essence, this modeling setup corresponds to reducing the width of the time window over which a particular host species is suitable for oviposition. For instance, if the insect is a leaf-specialist, then a particular host plant species may be suitable during all ten periods of a reproductive season, whereas, if the insect is a seed pod specialist, that host species may only be suitable for oviposition during five of these ten periods. This approach to modeling the availability of suitable hosts as time windows of varying width in a given season was inspired by the empirical findings of Wiklund and Friberg ([127]—see section 5.1).

In this model scenario, suitable hosts of each species could be present during 2, 3, 5, 8, or all 10 periods of a season. For greater intuitive clarity and a closer connection to biological reality with its early- and late-flowering host plant species (see section 5.1), I let one host be present in a continuous time window at the beginning of the season and the other at the end of the season. For the case of 8 periods with suitable hosts, for instance, host one was present during the first eight periods, host two during the last 8 periods, and both hosts were thus present simultaneously in the central 6 periods. Note that this assumption is likely to give a less conservative estimate for the evolution of generalism compared to when both suitable hosts are always present together. This is because, as discussed previously, the model assumes that insect fecundity is divided evenly across all periods of a season. As a result, periods with only the low-quality host species confront insects with the ultimatum of either using this host or laying no eggs at all, whereas periods with both hosts leave insects with the option of choosing one or the other. Moreover, in contrast to my two previous approaches, the total number of hosts encountered during a season (i.e., the total abundance of suitable hosts) varies alongside the number of periods with suitable hosts. I chose not to correct for variation in total host abundance out of biological realism—necessarily, the number of suitable hosts of a given species encountered by an insect during a reproductive season decreases if that host is suitable for oviposition during fewer season periods.

The results demonstrate that, as expected, insect acceptance rates of a lower-quality host increase as the number of periods with suitable hosts decreases (figure 5.7, top row). This effect holds when host quality varies in terms of either carrying capacity or larval performance. The increased acceptance of low-quality hosts is because an insect's risk of not being able to lay all its eggs—i.e., of becoming time-limited—increases when the insect encoun-

ters fewer suitable hosts during a reproductive season. Therefore, the insect's reproductive success may benefit from also laying eggs on low-quality hosts once host abundances have become sufficiently low. Simply put, laying an egg on a bad host is better than not laying an egg at all.

The observed threshold behavior is reminiscent of the scenario when I varied host abundance in a single-period season (compare figure 5.4 and 5.7, top rows). Indeed, one major effect of shorter time windows with suitable hosts for oviposition is to simply reduce average encounter rates with suitable hosts over the course of a season. In order to examine this effect in more detail, I compared the evolutionary response of insect acceptance rates when host abundance varies in terms of number of periods with suitable hosts in a *multi-period* season compared to when it varies in terms of number of hosts encountered in a *single-period* season. The results show that, generally, insect acceptance rates of the lower-quality host do not differ between the two treatments (see figure 5.7, bottom row). These findings suggest that phenological specialization can make wider diet breadths adaptive simply because, if hosts are only suitable during a certain stage of their phenology, then insect encounter rates with suitable hosts shrink accordingly (see [127]). At least with the current parameter settings, the additional "pessimistic" response to hosts being spread out over more time periods does not make much of a difference (compare figure 5.5).

5.4.4 Results summary

The results presented above paint a clearer picture of how seasonal host distribution patterns affect insect oviposition decisions. Most importantly, the simulations demonstrate that such shorter time windows with suitable hosts as would result from phenological specialism can lead to the evolution of generalist oviposition strategies. In line with previous speculation, the results suggest that this evolutionary response is due to phenological specialism decreasing the perceived abundance of suitable hosts. Moreover, the simulation results show that periods with fewer than average hosts lead to insects increasing their acceptance rates so that they can still lay sufficient eggs despite decreased encounter rates. This evolutionary effect, however, is only apparent if the quality of the two host species is similar. Otherwise, these adaptively pessimistic effects are soon outweighed by the costs of laying more eggs on lower-quality hosts.

5.5 Discussion

In this chapter, I present the results of a simulation model to assess the hypothesis that the higher degree of phenological specialism in the seed-eating larvae of the orange tip butterfly (*Anthocharis cardamines*) has lead to a greater degree of oviposition generalism in adult females of that species. In the context of these individual-based simulations, insects encountered host species which differed in quality either in terms of larval survival or in terms of the degree of larval competition as determined by the host species' carrying capacity. I then searched for conditions where lower-quality hosts would be accepted for oviposition and thus included into the butterfly's diet breadth, that is, where generalist oviposition strategies would evolve.

The simulations results demonstrate that competition among surviving larvae often has stronger influence on female oviposition preferences than larval survival rates on different host plant species. Moreover, as expected from analytical results of previous chapters, the

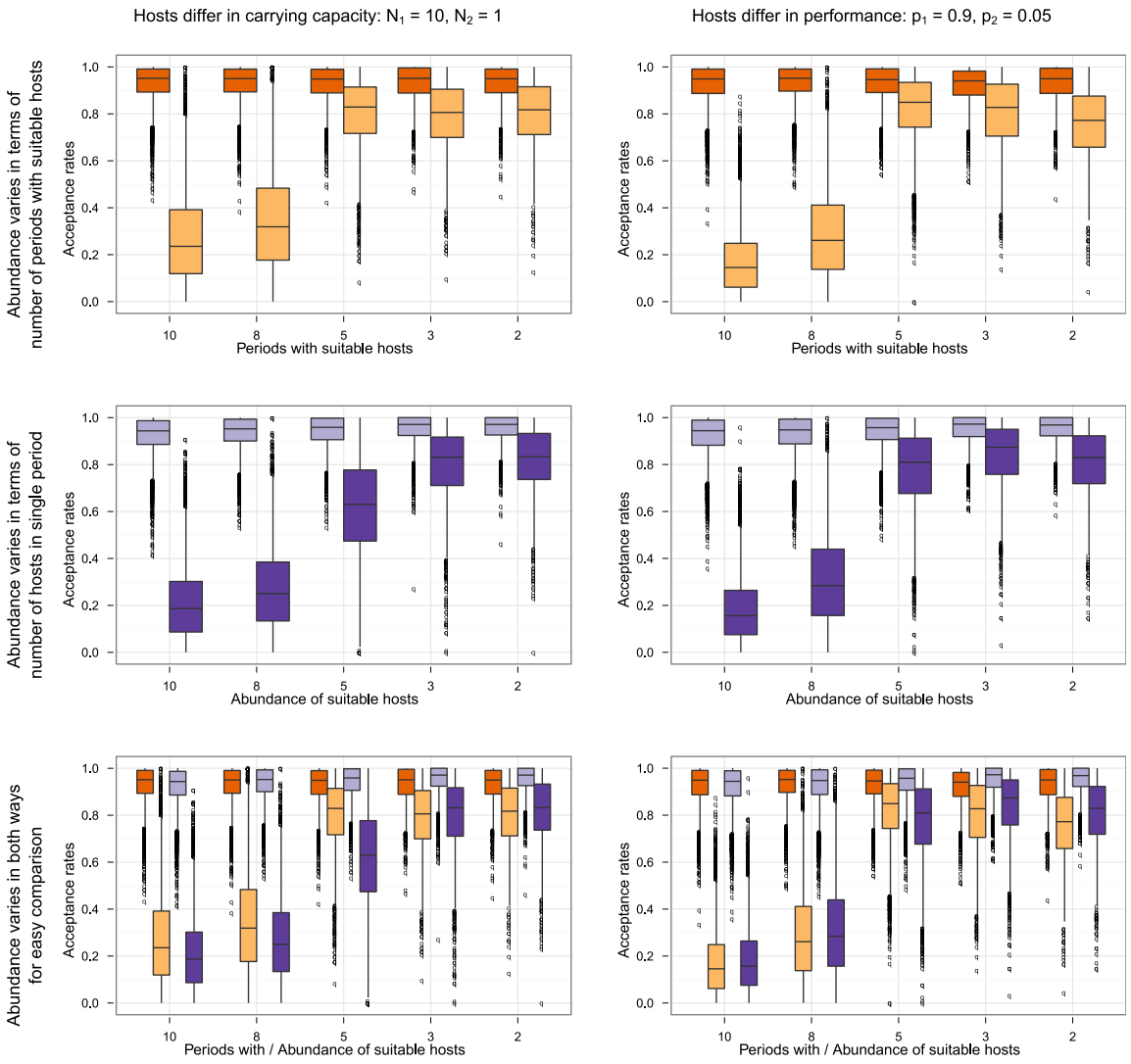


Figure 5.7. Effect of reduced temporal host availability on acceptance rates of host species with different quality. The top row shows acceptance rates of two host species of different quality (dark orange, higher quality; light orange, lower quality) when the number of periods in a ten-period season varies where suitable hosts are encountered (at an average rate of one per period). The mid row shows the same acceptance rates (light purple, higher quality; dark purple, lower quality) when total abundance of suitable hosts is varied within a *single-period* season. The bottom row summarizes the top two rows for comparison. The left column varies host quality varies in terms of carrying capacity (larval performance on both host species set to 1); the right column in terms of larval performance (carrying capacity set to 10). Simulations were run for 1000 generations in 100 well-connected patches (migration rate of 90%) with a total carrying capacity between 22 and 200 per patch, depending on carrying capacities and abundances.

simulation results demonstrate that host acceptance rates rise if females are more likely to be limited by the number of hosts they encounter than by the number of eggs they carry—that is, when they are more likely to be time- than egg-limited. The simulation results also showed an evolutionary response of female oviposition strategies to different host distribution patterns across a reproductive season, where acceptance rates increased if hosts were rarer during certain periods of a season. This effect of host abundance patterns on female acceptance rates of host species was most distinct when females encountered host species of *equal* quality but less so when they encountered host species of *different* quality. Finally, the simulation results demonstrated that phenological specialism can indeed lead to wider diet breadths in individual insects. This effect is mediated by the lower perceived availability of suitable hosts which, again, is due to greater phenological specialization. Furthermore, this effect of lowered encounter rates is hardly augmented by insects encountering fewer hosts in each period of a multi-period season compared to when they encounter the same number of hosts combined in a single-period season.

5.5.1 Comparing model results with empirical findings

In field observations, females orange tip butterflies were prone to oviposit on any of their cruciferous host plant species without apparent differences in oviposition preferences [126]. Judging from my model results, this suggests that differences in quality between different host species may to not be large enough to warrant differential host acceptance rates. Alternatively, as has been suggested by Wiklund and Åhrberg [126], the absence of preference-performance correlations with regard to host plant species identity could be due to other environmental factors affecting larval performance to a greater degree than species identity.

Preferences with regard to additional plant characteristics other than host plant species identity were detectable in the field, however. Generally, these findings confirm the expectations from the orange tip larvae's phenological specialization on seed pods: (1) Females orange tip butterflies only oviposited on host plants in bloom; (2) females preferred host plants with young inflorescences and rejected aged inflorescences for oviposition on several occasions; (3) females preferred host plants with sufficiently strong stems—a plant feature potentially allowing insects to assess the future availability of seed pods as larval food on this stem by way of that stem's size and stability [126]. A correlative study that retrospectively compared the use of different host plants for oviposition by orange tip females found similar results with higher floral area and larger stem size correlating with the number of eggs found on a given plant [2]. Although plant characteristics pertaining to phenological state were not included in the present version of the simulation, they could form an insightful part of future model extensions (see below).

In addition to their preferences for specific host species and specific host phenological stages, female orange tip butterflies were observed in the field to consistently reject those host plants for oviposition that already contained an orange tip egg [126]. This rule is apparently broken only rarely with far fewer hosts containing more than one orange tip egg than expected by chance alone [126]. In the simulation, the use of individual host plants was not modeled explicitly, and females could thus not assess whether a host had been oviposited on before. Generally, however, such behavior is in line with the effect of competition on the different host species detectable in the simulation results (see figures 5.2–5.4). Indeed, there is circumstantial evidence that competition for food does occur among orange tip larvae on a host plant—usually, only one larvae develops successfully on a given flower head, probably also because of the larvae's previously described cannibalistic behavior [20].

A productive empirical point for comparison with the orange tip butterfly's oviposition strategy comes from pierid butterflies such as *Pieris rapae*. This common butterfly species belongs to the same family as *Anthocharis cardamines* and lays eggs on some of the same host species. Its larvae, however, feed not on seeds but mostly on leaves. As a result, adult *P. rapae* require host plant individuals with sufficient leaf-area, independent of these plants' seed availability, and show a smaller diet breadth than *A. cardamines* (e.g. [59]). Moreover, ovipositing *P. rapae* females should be less constrained by time compared to *A. cardamines* because time windows for host plants possessing large leaf areas are larger than for plants containing sufficient numbers of mature seed pods. In the context of the simulation model, *P. rapae* could be represented as a species with wide time windows of host suitability and thus high perceived rates of host encounter, whereas *A. cardamines* is characterized by narrower windows of host suitability and accordingly lower perceived rates of host encounter. Framed in this way, the model results that lower perceived host availability can lead to an increase in diet breadth are in line with the empirical finding that *A. cardamines* accepts more hosts for oviposition than does *P. rapae*.

Another interesting point of comparison may come from a different Anthocharis species, *Anthocharis euphenoides*, home to Spain, southern France and central Italy. This species is described as being monophagic on its brassicaceous host *Biscutella laevigata* where, like *A. cardamines*, its larvae preferably eat seed pods and flowers [101]. This monophagy on a single plant contrasts with the wide diet breadth of *A. cardamines*. Similar to the case of *Pieris rapae* presented above, my model results generate a plausible hypotheses as to why *A. euphenoides* can afford to be monophagic on a single host plant and yet still be a phenotypic specialist with seed-eating larvae: Most likely, the availability of hosts is predictably high across seasons, either because hosts simply are very abundant or because hosts carry mature seeds for longer periods of the insects' flight period so that the time window of host suitability becomes wider. Though somewhat speculatively without more precise data, the latter hypothesis derives support from the fact that *A. euphenoides* lives at more southerly latitudes than *A. cardamines* and may therefore enjoy a less seasonal climate with less inter-annual variation.

5.5.2 Significance for future empirical research

The model results presented in this chapter suggest different routes for future empirical research. Hypotheses generated by the model could be tested experimentally or through correlative field studies. Moreover, empirical studies could be designed in tandem with future extensions to the current simulation model (see section 5.5.4).

The model predicts, for instance, that the species identity of a given host plant should affect the insect's oviposition decision in accordance with that host species' quality. Conversely, current field data finds that host quality and oviposition acceptance are only poorly matched in the orange tip butterfly [127], but that strong effects of such phenological traits as flower number and shoot size are apparent [2, 3]. These contrasting findings suggest that the phenological status of a given host plant is likely able to override the effect of that plant's species identity. Simply put, insects may prefer a bad host with many flowers to a good host with few flowers. It may therefore be fruitful to assess empirically how a plant's phenological state and its species interact to determine an insect's oviposition decisions. This could be done, for instance, by presenting individual ovipositing females in cage experiments with a number of hosts of different species and different phenological states and recording each female's oviposition behavior. While the current simulation model implicitly assumes that

phenological states affect oviposition decisions through reduced encounter rates of suitable hosts, future versions that consider separately the inputs of state and species identity could benefit greatly from such empirical studies.

The model also predicts that insects adapt to varying host abundances in their oviposition strategies. This straightforward finding is not new empirically (e.g. [112]). Nevertheless, it suggests that assessing the oviposition preferences of orange tip butterflies in different areas within their large geographical range may present a promising area of research. Empirical efforts to this end are already under way at different locations in Sweden with different host plant distribution (Johan Ehrlén, pers. comm.). Comparing these results with model predictions may necessitate placing the model within a spatially explicit context to account for gene flow between populations with varying host encounter rates. Alternatively, the insects' oviposition preferences could also be phenotypically plastic, affected by such geographically varying factors as light or temperature, so that one plastic strategy may produce different oviposition preference at different latitudes and/or altitudes.

Finally, the model makes clear assumptions as to what orange tip butterflies "see" in their environments. In the current model implementation, for instance, butterflies always reject phenologically insufficient hosts for oviposition (as indirectly follows from their reduced encounter rates). In the field, this behavioral switch is likely to be less strict, and many factors probably influence each oviposition decision (compare section 5.5.4 and figure 5.8). As a result, the model presents the opportunity to include other specific inputs to oviposition and compare the resulting oviposition preferences and egg distributions with suitable field data where not only host species identity but also such phenological variables as shoot height, flower number, of number of seed pods have been recorded. In combination, theoretical and empirical approaches could therefore allow the identification of relevant environmental factors in insect oviposition decision making.

5.5.3 Patterns of environmental variation

The patterns of environmental variation in time and space of such factors as host availability or seasonal temperatures are of fundamental importance to strategic insect oviposition. Insightful work by John McNamara and colleagues on adaptive optimism and pessimism has shown that, due to the geometric nature of reproduction, lineages adapt disproportionately to conditions *better* than the average when varying conditions affect lineage members *similarly*, whereas they adapt disproportionately to conditions *worse* than the average when varying conditions affect lineage members *individually* ([75]—see also section 1.4 on page 7 of chapter 1). The former is the case when variation in the relevant factor is spatial, the latter when variation is temporal. While spatial variation is absent from the simulations presented here, the results demonstrate the expected effects of temporal variation with insects adjusting host acceptance rates disproportionately to conditions in periods with less than average host encounter rates, at least when these effects are not masked by differences in host quality (compare figure 5.5).

Temporal autocorrelation

In any real-world ecosystem, variation of environmental factors can always be described in terms of the distributions that these factors are said to lie within. For instance, a classic result in ecology (which has necessarily been challenged since its publication) demonstrated that species-abundance distributions usually follow a log-normal distribution [87].

The values of biotic and abiotic factors, however, are not simply drawn from some underlying distribution. Instead, the value of a given factor in a given year contains information on the value of that factor in pre- and succeeding years—that is, random variation in the environmental is temporally auto-correlated (usually with a bias towards positive autocorrelation in marine environments but without such a bias in terrestrial ecosystems—[117]). While the presence of auto-correlation is unsurprising in time-series with underlying autoregressive dynamics such as populations of animals or annual plants, this phenomenon is less easily explained in time-series relating to climate, for instance the North Atlantic Oscillation [98].

Theoretical models have demonstrated that the effect of autocorrelation on growth rates of structured populations can be larger than that of interannual variability [114], and experimental results show that increasing temporal autocorrelation can accelerate extinction [86]. As a result, a greater role for the effects of environmental autocorrelation in studies of both ecological and evolutionary dynamics has been advocated [98].

In the simulation model presented in this chapter, auto-correlation was absent from the model's input of host abundance patterns, and environmental variation was therefore uncorrelated. Nonetheless, it may be rewarding to speculate how between-year correlations in host availability may affect insect oviposition strategies. If abundances of host plants are positively auto-correlated—as seems to generally be the case in annual plants, though not in the growth rates of perennial plants, which are negatively auto-correlated [10]—then periods of sustained high as well as low abundance are longer than expected by chance. In the short run, insects would therefore profit from adapting their strategies to periods of high host availability during these periods, but would also incur higher costs during periods of low host availability unless they adapted their strategies to those periods.

In the long run, the geometric mean fitness of any oviposition strategy necessarily remains unchanged as long as only the correlative structure of the environmental variation changes but not its mean and variance. As a result, such genetically hard-wired oviposition strategies as are examined in my simulation model are unlikely to evolve to make use of positive autocorrelation in host availability. However, phenotypically polymorphic oviposition strategies, which were not the focus of this study, could be able to exploit such auto-correlated environments because variation present at polymorphic loci may allow inferences from the recent past on the short-term future of the respective environments [66]. As a result, correlated environmental variation could form an insightful part of future simulation studies on strategic oviposition that include the possibility of such phenotypic polymorphism. These approaches could be especially interesting because phenotypic polymorphism in oviposition strategies could mark the beginning of host race formation [123], which has in turn been identified as an important factor in sympatric speciation [23].

Effects of interannual variability

As a result of these considerations on the patterns of environmental variation, it would be particularly interesting to consider the effects of inter-annual variation in mean host plant availability in future versions of the model. Temporal variation likely increases the benefits of including lower-quality hosts in one's diet because doing so protects individuals from particularly low fitness returns in years when high-quality hosts are unusually rare.

In this context, widening the insects' diet breadth carries the additional benefit of decreasing perceived inter-annual variation in the combined availability of all host species as long as the hosts' reaction norms with regards to temperature vary between host species. This is

because, if host species react differently to varying temporal conditions and an insect accepts several host species for oviposition, this insect is more likely to encounter at least some of its hosts even if temperatures in a given season are unusually high or low.

Taken together, these facts illustrate why generalist oviposition strategies in the face of temporal variation resemble bet-hedging: By enlarging their diet breadth, female butterflies reduce the variance in reproductive success by reducing mean reproductive output. In a sense, additional host species in the diet breadth act as a safeguard so that, when a female misses the narrow time window of the original host, she can still reproduce successfully on these extra hosts. In the orange tip butterfly, such bet-hedging strategies have indeed been hypothesized to occur as a product of larval survival on different host plant species varying unpredictably between years [127].

5.5.4 Possible future extensions to the simulation

In future work, further details could be added to this individual-based simulation due to its inherently modular structure. Among the options presented in figure 5.8, explicitly modeling additional plant traits such as phenological state and taking these as input to the butterfly's oviposition decisions seems especially rewarding. At the same time, the strategic output of butterfly behavior could be expanded to include responses not only to host species identity but also to host phenological state and other plant characteristics. In this way, one could gain more insights into the decision mechanisms that underly the oviposition patterns observed in the field, such as the hierarchy threshold model proposed by Courtney and colleagues [16].

Additionally, it could be worthwhile to explore the different ecological situations that are faced by orange tip females in different parts of their range. This is because ovipositing orange tip females show realized preferences that differ over their large geographical range (Tenna Toftegaard, unpubl. obs.). It seems therefore possible that the orange tip's oviposition preferences are modulated by local conditions, as would be expected if geographically varying parameters like temperature play a large role in host plant quality. Such inputs were disregarded in the current simulation but could be included into future versions of the model. Interestingly, the preferences of orange tip females for specific phenotypic stages of their host plants have been shown to occasionally diverge between host species with females preferring early individuals in one species and late individuals in another (Jose A. Navarro, unpubl. obs.). This finding implies that, similarly to the case of preferences being modulated by local conditions, an individual butterfly's assessment of the phenological stages of a given host plant would have to be modulated by the species identity of that plant.

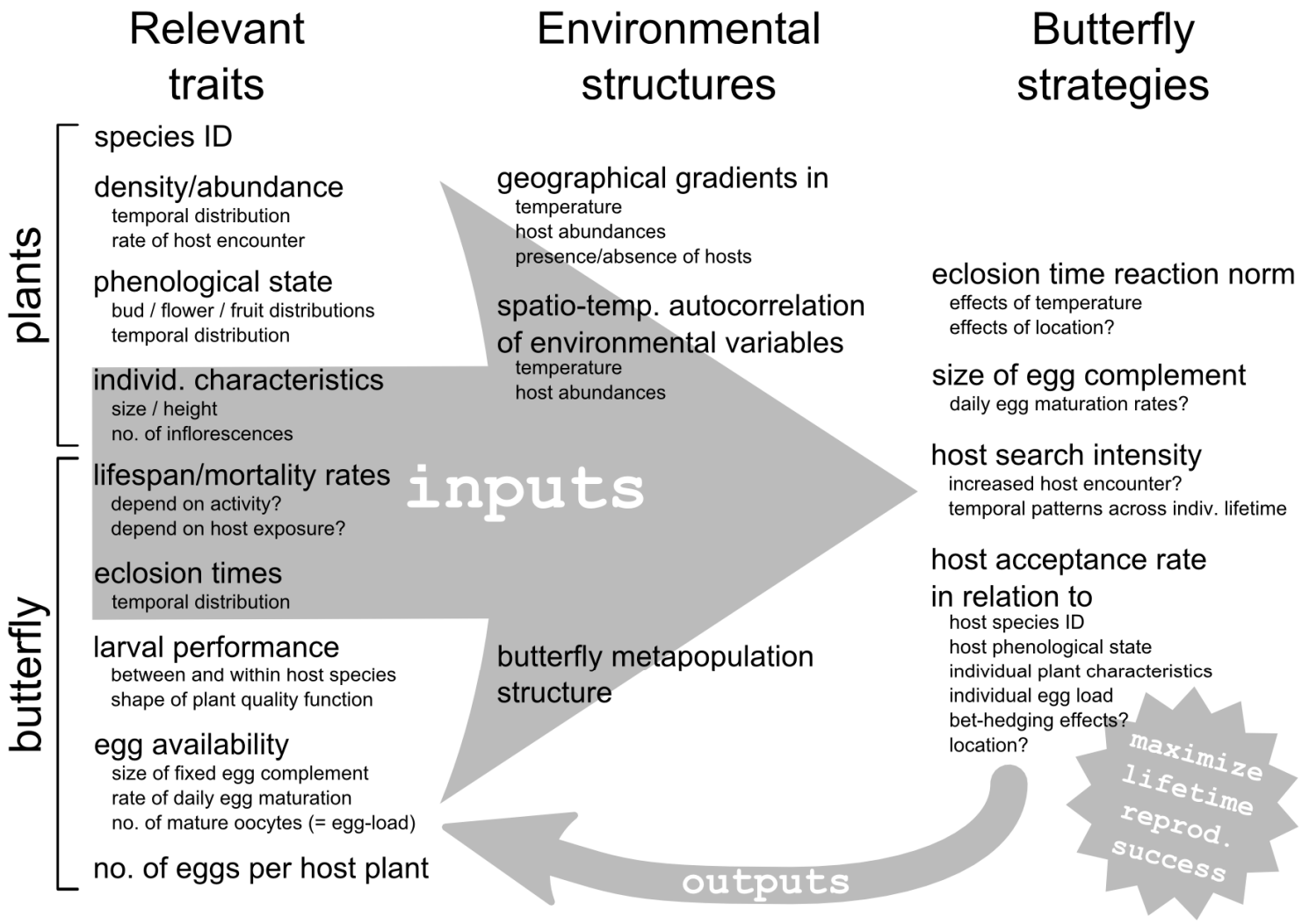


Figure 5.8. Schematic diagram highlighting possible extensions to the simulation model (see section 5.5.4).

5.5.5 Beyond the black box: Simulations as cognitivist approaches to insect oviposition?

Since the cognitive mechanisms underlying insect oviposition behavior are difficult to assess experimentally, extended versions of the simulation study presented in this chapter may present the opportunity to assess such mechanisms in more detail *in silico*. Generally speaking, cognition is the neuronal acquisition, retention, and use of information [24]. Cognitive analyses thus assume three distinct steps to occur "inside the black box:" (1) external information is filtered, encoded, and stored; (2) this stored information is manipulated; and (3) a particular internal 'representation' is generated from the manipulated input that specifies which action must take place [91].

The subjectively constructed representations that are generated by cognitive processes are the product of adaptation and constraints [91]. In this sense, evolution creates algorithms for appropriate—i.e. task-specific—representations of environmental patterns given external and internal inputs as well as cognitive constraints. Many studies indicate that genetically based individual variation for cognitive traits exists, that cognitive traits affect individual fitness, and that cognitive traits thus evolve (reviewed in [24]). Specifically, different representations of the same external input can have different fitness consequences [91] since these representations map external information more or less efficiently and more or less accurately. As a result, internal representations are expected to always be "adequate" in the sense that they reflect an organism's informational needs.

Cognitive abilities are likely fine-tuned to an organism's life history requirements because of its limited cognitive capacities. This is a "cost-benefit under constraints" argument where cognitive capacties are limited by network size—viz. computational power of the system—which would be costly to enlarge. As a result, metabolically expensive neuronal tissue is allocated in response to behavioral and environmental needs, and the cost of cognition is thus balanced against the fitness consequences of the respective cognitive traits [24]. In birds, for example, comparisons between storing and non-storing species of tits (*Parus spec.*) show storing species to have better spatial memory, while in mammals, less sedentary voles (*Microtus spec.*) have superior spatial abilities compared to more sedentary species (reviewed in [41]). In insects, a solitary and a social bee species (*Xylocopa virginica* and *Bombus bimaculatus*) were shown to differ in their learning abilities in ways consistent with differences in their life histories [25]. Generally, the trade-off hypothesis on cognitive abilities predicts closely related species with different autecologies to possess correspondingly different cognitive abilities.

Plasticity and learning also play a—expectedly significant—role in determining cognitive abilities. For example, sticklebacks from stable environments perform better in maze orientation experiments if they are given landmarks, whereas fish from unstable environments perform just as well without the help of such landmarks [37]. Mechanistically, past experience may feedback on neural structures as has been shown for marsh tits (*Parus palustris*) where food-storing is necessary for hippocampal expansion [13]. Effects of environmental enrichment on brain and behavior have also been documented in fruit flies [24]. Even though cognitive capacities are likely the product of both computational and ecological constraints [41], not all cognitive capacities necessarily trade-off against each other. In fruit flies under strong artificial selection for aversive learning, for example, the "bright" line showed not only an increase in learning rates but also a decrease in memory decay [77].

Cognitive implementations of optimal insect oviposition

A number of cognitive mechanisms relevant to optimal oviposition strategies could be explored in future, enlarged versions of the individual-based simulation (see section 5.5.5 and figure 5.8). The probabilities of encounter with different host plant species, for instance, could be estimated in terms of delay between events so that probability perception becomes an implicit function of patterns of temporal perception [91]. Such cognitive abilities to estimate rates and probabilities would therefore depend on an organism's ability to encode numerosity of objects as well as their temporal sequence—these capabilities would have to be made explicit as assumptions to the simulation. Moreover, biases in probability estimation can arise due to the process of information encounter as well as due to system-inherent memory decay. In fact, memory dynamics may even generate such time-lagged responses as have been observed in individual bumble bees who switch floral preferences in response to artificial changes in relative flower abundance [91]. It is possible that memory dynamics can also be used as part of oviposition strategies, for example when assessing oviposition or host encounter rates. If the memory decay rate of past encounters with a given host plant depends on specific details relevant to that plant's quality as an oviposition site such as species identity or phenological state, then this could result in internal representations biased towards encounters with high- or low-quality hosts—*"forget encounters with bad hosts, remember those with good hosts."*

But the cognitive implementation of insect oviposition strategies could begin far below the step of memory formation and decay. The first step in information-processing is always information input. Thus, perception plays an important role in shaping cognitive outputs. As a result, preference shifts in insects could be the result of changes at the perception level instead of at higher cognitive levels. In support of this hypothesis, several studies have found genetically based individual variation in response to various odors in fruit flies (reviewed in [24]). Smells and odors are likely to be key factors in host plant recognition and assessment. Within the context of the simulation study, the perception of key plant traits such as phenological state—potentially assessable as the number and/or size of buds, flowers, and fruits—could be explicitly included into an individual's behavioral program. By comparing actual egg-distribution patterns in the field with the resulting oviposition patterns from the model as well as with results from simulation versions not considering these perception details, one could then estimate the importance of plant quality perception for strategic insect oviposition in the wild.

Specifically, the orange tip system may present the possibility to study the decision making mechanism underlying the butterflies' oviposition strategies. For instance, orange tip females prefer larger flower shoot sizes in certain hosts, but this preference may be absent in other host species (for instance, it is present in tetraploid but absent in octaploid *Cardamine pratensis*—[2]). At the same time, phenologically unsuitable individuals of an, on average, high-quality host species are preferred to a lesser extent than phenologically more suitable individuals of an, on average, low-quality host species. As a result, if one presupposes an internal ranking mechanism where plants are accepted if some hypothetical "score" has reached a hypothetical "threshold" (as in Courtney's hierarchy-threshold model [16] and as would be expected in sequential choice tasks like this one), then the scoring would have to be based on an interaction between host species identity and factors indicating a host plant's phenological state. Such factors could include direct measures like the number or size of inflorescences as well as derived measures like the ratio of seed pod number over the sum of seed pods and flower number.

5.5.6 Conclusion

Using the example of the orange tip butterfly, the simulation results presented in this chapter give support to the hypothesis that the larvae's phenological specialism makes adaptive the adult butterflies' generalist oviposition strategy. Moreover, the results suggest that, as indicated by empirical results, competition among larvae for survival is likely to have a large influence on optimal oviposition strategies. As a result, even though the simulation is still relatively schematic compared to the degree of complexity apparent in empirical data on orange tip oviposition behavior, the results presented in this chapter demonstrate the great potential for individual-based simulations to examine questions of strategic oviposition in specific ecological scenarios.

In particular, future simulations could be extended in two directions, either "externally" by implementing in more detail the relevant environmental variation, their patterns, and their effects on host and insect abundances, or "internally" by mapping in more detail the decision making mechanisms of ovipositing insects and their assessment of potential host plants. Either of these theoretical routes is capable of producing insights into strategic insect oviposition behavior that are hardly extractable from current empirical data.

6 Conclusion and outlook

The last five chapters have demonstrated the intricacy of how decision problems arise and are solved by phytophagous insects. During oviposition, insects are constantly faced with the problem of accepting lower-quality hosts for oviposition or waiting out for higher-quality options. As a result of their oviposition choices, insects may run out of eggs before their lifetimes are over because they do not possess infinite resources. At the same time, insects may run out of time before all their eggs are laid because they are not immortal and because mortality is stochastic. The resulting risks of egg and time limitation determine the opportunity costs associated with every oviposition decision and thus shape insect oviposition strategies. However, using time and egg costs as a tool to investigate these strategies proves no less complicated than applying more direct optimization models.

How then to best approach the evolutionary analysis of when and where insects should lay their eggs? The results presented in this thesis suggest that the most straightforward methods are analytical optimization models coupled with more complex individual-based simulations. Since my analyses demonstrate that the effects of neither egg nor time limitation can safely be ignored in the study of strategic oviposition, such models should not pre-suppose either of these phenomena but instead treat egg and time limitation as the dynamic outcomes of oviposition strategies that they are. In this way, theoretical models can deliver insights on strategic insect oviposition that would hardly have been extractable from empirical observations alone.

One of the key problems in the study of insect oviposition is how increases in diet breadth come about—that is, how generalism can evolve from specialism. Most insects are relatively specialized in their oviposition preferences, yet temporary phases of generalism are the most plausible explanation for the many host switches indicated by phylogenetic analyses of plant-insect co-evolution. The results of my studies confirm the previous notion that unreliability of resources, specifically the availability of appropriate hosts, may drive females to include novel hosts into their diet breadth that are less suitable for larval development than previously preferred hosts.

My findings stress, however, that this effect depends crucially on whether the unreliability of host availability occurs in space or in time. If host availability varies in space, generalism does not necessarily evolve because differences in productivity between habitats can lead to source-sink dynamics which favor specialist oviposition strategies that produce high reproductive payoffs only in high-quality habitats over generalist strategies that produce lower reproductive payoffs in both high and low-quality habitats. If host availability varies in time, however, insects may indeed fare better with more generalist oviposition strategies that also produce high reproductive payoffs in times when high-quality hosts are rare or absent. As my simulation results confirm, the oviposition generalism of the orange tip butterfly (*Anthocharis cardamines*) may be an example of such an evolutionary response to temporally varying host availability because the orange tip larvae's specialization on flowers and seeds shortens the time window during which each host plant is suitable for successful larval development.

In summary, general conclusions on optimal oviposition strategies that are valid across all

phytophagous insects will be hard to draw from such theoretical studies as are presented in this thesis. However, predictions for the strategic oviposition behavior of particular species can be made based on a number of ecological and developmental factors. My results suggest that the availability of suitable hosts and their variation in time and space is likely the most crucial of these factors. At the same time, the shape and parameters of the life-history trade-off between survival and reproduction are also of key importance because this trade-off determines the risks of time and egg limitation which, in turn, dynamically influence the fitness costs and benefits of each oviposition decision. In general, these findings showcase how theoretical models can provide a helpful tool to elucidate the strategic oviposition behavior of phytophagous insect species where detailed knowledge on ecology and development is available or at least empirically accessible.

In the future, the studies presented in this thesis may provide a starting point for several promising research projects. Especially the simulation study with its inherently modular structure lends itself to expansions that could, for instance, explore more cognitivist approaches to strategic insect oviposition such as the hierarchy-threshold model. But expansions could also be made to the study of strategic oviposition in the face of spatial heterogeneity, for example with regards to the evolution of dispersal strategies. More generally, the co-evolution of larval performance with adult preferences and their combined effect on strategic oviposition could be a fruitful topic for future modeling studies, especially in the context of the *"jack of all trades—master of none"*-hypothesis. In short, there remains much to be done in the theoretical study of strategic oviposition in phytophagous insects.

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Than it nibbled a hole in the cocoon, then it pushed his way out and...
It was a beautiful butterfly.
Eric Carle, The very hungry caterpillar

Selbständigkeitserklärung

Ich erkläre ausdrücklich, dass es sich bei der von mir eingereichten schriftlichen Arbeit mit dem Titel "When and where to lay your eggs?" um eine von mir selbstständig und ohne fremde Hilfe verfasste Arbeit handelt.

Ich erkläre ausdrücklich, dass ich *sämtliche* in der oben genannten Arbeit verwendeten fremden Quellen, auch aus dem Internet (einschließlich Tabellen, Grafiken u. Ä.) als solche kenntlich gemacht habe. Insbesondere bestätige ich, dass ich ausnahmslos sowohl bei wörtlich übernommenen Aussagen bzw. unverändert übernommenen Tabellen, Grafiken u. Ä. (Zitaten) als auch bei in eigenen Worten wiedergegebenen Aussagen bzw. von mir abgewandelten Tabellen, Grafiken u. Ä. anderer Autorinnen und Autoren (Paraphrasen) die Quelle angegeben habe.

Mir ist bewusst, dass Verstöße gegen die Grundsätze der Selbstständigkeit als Täuschung betrachtet und entsprechend der Prüfungsordnung und/oder der Allgemeinen Satzung für Studien- und Prüfungsangelegenheiten der HU (ASSP) geahndet werden[1].

Datum: Unterschrift:

[1] Diese Erklärung stammt von der Seite der philosophischen Fakultät II der Humboldt-Universität zu Berlin, abrufbar unter `http://fakultaeten.hu-berlin.de/philfak2/lehre/Promotion_Habil/download/selbststandigkeitserklarung_promo.pdf` [abgerufen am 2.4.2013].